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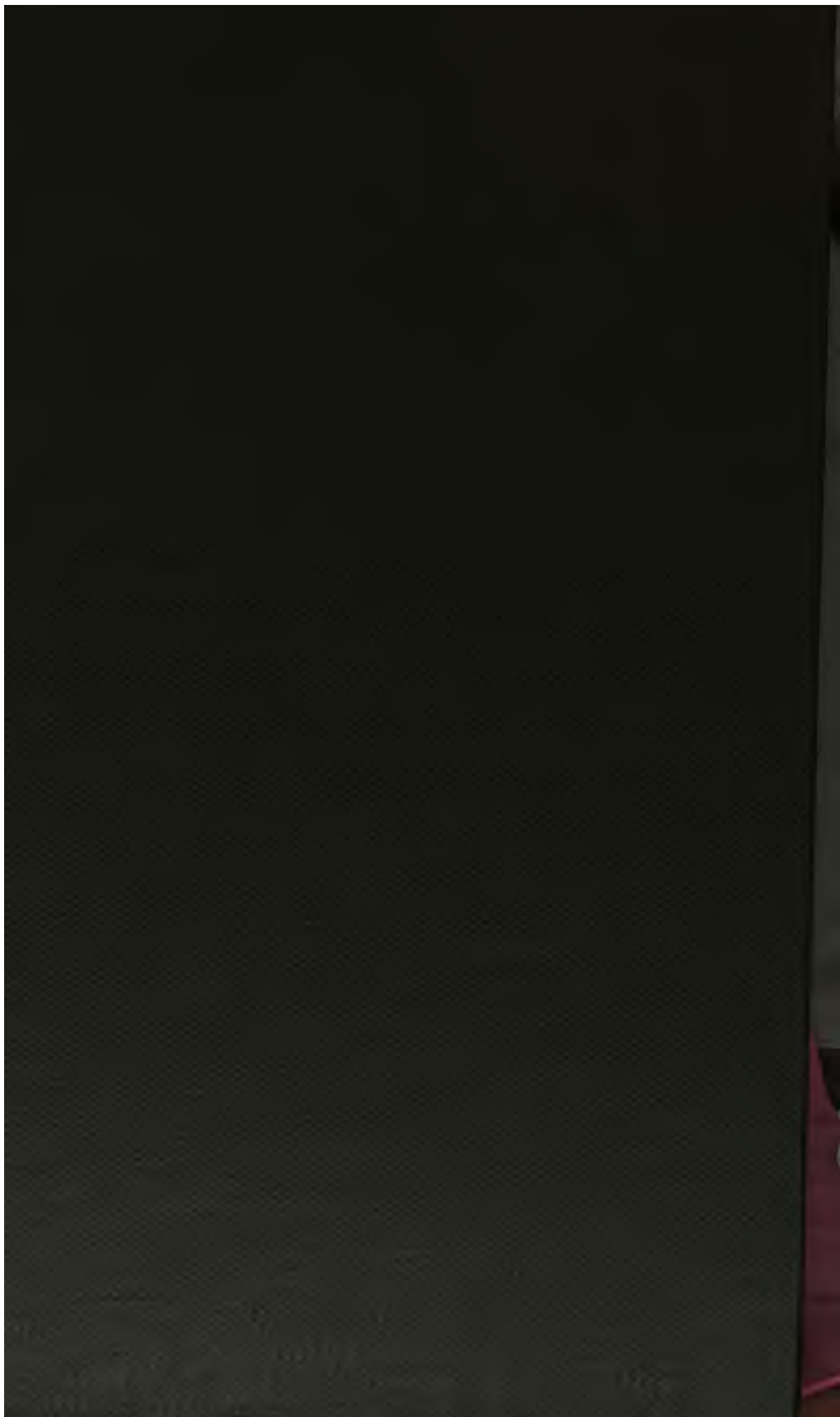
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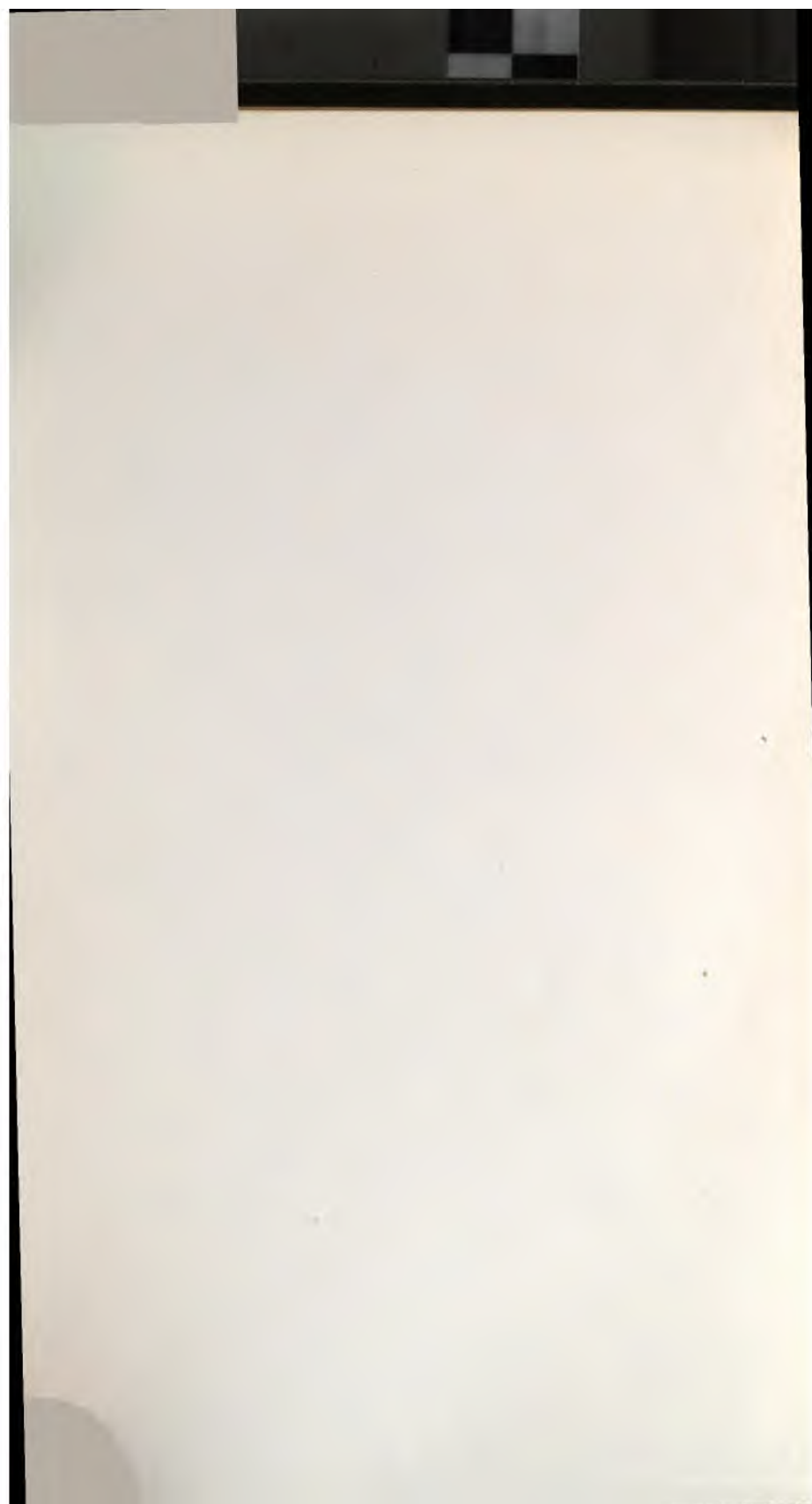
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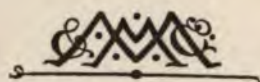






**E. Saunders,**

**THE FERTILISATION OF FLOWERS**



THE  
FERTILISATION OF FLOWERS

BY  
PROF. HERMANN MÜLLER

TRANSLATED AND EDITED BY  
D'ARCY W. THOMPSON, B.A.  
SCHOLAR OF TRINITY COLLEGE, CAMBRIDGE

WITH A PREFACE BY  
CHARLES DARWIN

*WITH ILLUSTRATIONS*

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## PREFATORY NOTICE.

THE publication of a translation of Hermann Müller's *Die Befruchtung der Blumen, &c.*, will without doubt be a great service to every English botanist or entomologist who is interested in general biological problems. The book contains an enormous mass of original observations on the fertilisation of flowers, and on the part which insects play in the work, given with much clearness and illustrated by many excellent woodcuts. It includes references to everything which has been written on the subject; and in this respect the English edition will greatly exceed in value even the original German edition of 1873, as Müller has completed the references up to the present time. No one else could have done the latter work so well, as he has kept a full account of all additions to our knowledge on this subject. Any young observer who, after reading the whole or part of the present work, will look, for instance, at the flower of a *Salvia*, or of some Papilionaceous or Fumariaceous plant, or at one of our common Orchids, will be delighted at the perfection of the adaptations by which insects are forced, unconsciously on their part, to carry pollen from the stamens of one plant to the stigma of another. Design in nature has for a long time deeply interested many men, and though the subject must now be looked at from a somewhat different point of view to what was formerly the case, it is not thus rendered the less interesting.

Hermann Müller has by no means confined his attention to the manner in which pollen is carried by insects or other animals from plant to plant, for wind-fertilised flowers have been carefully described by him; and several curious transitions from the one state to the other are noticed. He has also attended more closely than any one else to the many contrivances for self-fertilisation, which sometimes co-exist with adaptations for cross-fertilisation. For instance, he has discovered the singular fact that with certain species two kinds of plants are regularly produced, one bearing inconspicuous flowers fitted for self-fertilisation, and the other kind with much more conspicuous flowers fitted for cross-fertilisation. The flowers on the first-mentioned plants serve the same end as the curious little closed cleistogamic flowers which are borne by a considerable number of plants, as described and enumerated in the present work.

There is another interesting feature in the *Befruchtung*, by which it differs from all other works on the same subject; for it includes not only an account of the adaptation of flowers to insects, but of different insects to differently constructed flowers for the sake of obtaining their nectar and pollen.

Any one who will carefully study the present work and then observe for himself, will be sure to make some interesting discoveries; and as the references to all that has been observed are so complete, he will be saved the disappointment of finding that which he thought was new was an already well-known fact. I may perhaps be permitted here to mention a few points which seem to me worthy of further investigation. There are many inconspicuous flowers which during the day are rarely or never visited by insects, and the natural inference seems to be that they must be invariably self-fertilised; for instance, this is the case with some species of *Trifolium* and *Fumaria* which bear very small flowers, with some species of *Galium*, *Linum catharticum*, &c. Many other such flowers are enumerated by Müller. Now it is highly desirable that it should be ascertained whether or not these flowers are

visited at night by any of the innumerable individuals of the many species of minute moths. A lepidopterist while collecting at night, if endowed with only a small portion of the indomitable patience displayed by Müller, could ascertain this fact. The question possesses a considerable degree of theoretical interest; for if these inconspicuous flowers are never visited by insects, why, it may be asked, do they expand, and why is not the pollen protected by the petals remaining closed, as in the case of cleistogamic flowers? It would perhaps be possible to smear such small flowers with some viscid matter, and an examination of the petals would probably reveal nocturnal visits by moths by the presence of their scales; but it would be necessary to prove that the matter employed was not in itself attractive to insects. H. Müller gives long lists of the several kinds of insects which he has seen visiting various flowers in Germany; and it would be interesting to learn whether the same insects and the same proportional number of insects belonging to the different orders, visit the same plants in England as in Germany.

There are many other subjects which it is desirable that some one should investigate, for instance, by what steps heterostylysm (of which an account will be found in the present work) originated: and with trimorphic heterostyled plants we meet with a more extraordinary and complicated arrangement of the reproductive system than can be found in any other organic beings. In order to investigate this subject and several others, experiments in fertilisation would have to be tried; but these are not difficult and would soon be found interesting. For instance, there are some plants, the pistils and stamens of which vary much in length, and we may suspect that we here have the first step towards heterostylysm; but to make this out, it would be necessary to test in many ways the power of the pollen and of the stigma in the several varieties. There exist also some few plants the flowers of which include two sets of stamens, differing in the shape of the anthers and in the colour of the pollen; and at present no one

knows whether this difference has any functional signification, and this is a point which ought to be determined. Again, there are other plants, for instance, the common Rhododendron, in which the shorter stamens are more or less rudimentary, and it has been asserted that seedlings raised from pollen taken from the short and from the full-sized stamens differ in appearance; and it would be of importance to know whether they differ in their fertility or power of yielding seeds. It would also be interesting to learn whether in the plants, already alluded to, which produce two forms, one adapted for self-fertilisation and the other for cross-fertilisation, the reproductive organs have become in any degree differentiated, so that their action would not be perfect if the two forms were reciprocally crossed. Would a flower adapted for self-fertilisation yield a full complement of seed if fertilised by pollen from one adapted for cross-fertilisation; and *vice-versâ* with the other form?

But it would be superfluous to make any further suggestions. These will occur in abundance to any young and ardent observer who will study Müller's work and then observe for himself, giving full play to his imagination, but rigidly checking it by testing each notion experimentally. If he will act in this manner, he will, if I may judge by my own experience, receive so much pleasure from his work, that he will ever afterwards feel grateful to the author and translator of the *Befruchtung der Blumen*.

CHARLES DARWIN.

Down, February 6, 1882.

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## ERRATA.

- Page 34, line 9, from top, *delete the words* "of Umbellifers."
- " 43, Fig. 8, for "Licus," read "Sicus."
- " 55, line 7, from top, for "feathery hairs," read "stiff bristles."
- " 149, " 25, " " for "ureus," read "urens."
- " 166, " 13, " " for "Æsculus Pavia (rubicunda)," read "Æsculus (Pavia) rubicunda."
- " 171, in both tables, transpose the words, "In Low Germany," and "On the Alps."
- " 427, line 26, from top, for "Scopolia," read "Scopolina."
- " 437, " 2, " " for "Digitalitis," read "Digitalis."

Labellæ is, perhaps, a better name for the lobes at the extremity of the proboscis in Diptera, called *end-flaps* (German *Endklappen*) or *paraglossæ* in Part II.

# THE FERTILISATION OF FLOWERS.

## PART I.

### HISTORICAL INTRODUCTION.

IT was not until the close of last century that the true purport and significance of flowers began to be perceived. Christian Conrad Sprengel seems to have been the first to view the subject in the light of adaptation, and to show how all the colours, scents, and singular forms of flowers have some useful purpose. His book struck out a new path in botanical science, and its title, *The Secret of Nature in the Form and Fertilisation of Flowers Discovered*,<sup>1</sup> shows that the author was well aware of the importance of his discoveries. Setting out with the conception of a "wise author of nature who has not created one hair without a definite purpose," Sprengel contrived, by reflecting on apparently insignificant facts, to throw light on most important phenomena in the life of flowers. The gradual progress of his discovery, as he describes it in the introduction to his book, is worth recapitulating.

The inconspicuous hairs which cover the lower part of the petals of the wood cranesbill (*Geranium silvaticum*, L.), and beneath which drops of honey lie hid, led Sprengel in the year 1787 to the discovery that most flowers which contain nectar are so arranged that, while insects can easily reach it, the rain is prevented from doing so; and he came to the conclusion "that the nectar of these flowers is secreted for the sake of insects, and is protected from rain in order that the insects may get it pure and unspoiled." Starting from this conception, he next summer studied the forget-me-not

<sup>1</sup> *Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen* (Berlin: 1793).

(*Myosotis palustris*, L.), and speculated on the meaning of the yellow ring round the mouth of the corolla, which forms a pleasing contrast to the azure-blue of the limb; and he conceived the idea that this might serve to guide insects on their way to the honey. On examination of other flowers he found that coloured dots and lines and other figures occur especially at the entrance to the nectaries, or point towards it, and he was accordingly confirmed in this idea of *path-finders* or *honey-guides*. The next step was easy, and Sprengel could scarcely remain long without perceiving that, as the special colour of one part of the corolla serves to guide the insect after it has settled upon the flower, the bright colour of the whole flower serves to attract the notice of insects while still at a distance. So far, Sprengel had looked upon flowers as contrived simply for the use of insects, but the study of some species of iris, in the summer of 1789, led him to the further discovery that many flowers are absolutely incapable of being fertilised without the aid of insects; and so he concluded that the secretion of honey in flowers, its protection against rain, and the bright colours of the corolla are contrivances of use to the flower itself by bringing about its fertilisation by insects. Thus were laid the foundations of a theory of honey-containing flowers, which Sprengel enunciates in the following propositions: (1) These flowers are fertilised by some one species of insect, or by several species; (2) the insects, in approaching the honey, brush pollen from the anthers with various hairy parts of their bodies and convey it to the stigma. The application of this theory to the various plants that came within Sprengel's reach led to the production of the above-mentioned book, which is marked throughout by a wealth of patient observation and acute reasoning. In it the following five features are described in several hundred species of flowers, partly native and partly cultivated, as proof of the correctness of the theory:—

(1) A *honey-gland* or *nectary*, *i.e.* a part which elaborates and secretes honey; (2) a *honey-receptacle*, which receives and stores the honey secreted by the gland; (3) a contrivance to shelter the honey from rain (*Saftdecke*); (4) contrivances to enable the insect to find the honey easily (*Saftmal*); bright colour and extension of the corolla, odour, and above all coloured spots near the entrance to the honey-receptacles (*path-finders*); (5) the impossibility of mechanical fertilisation, *i.e.* spontaneous self-fertilisation, or of fertilisation by the wind, and in many cases the direct observation of fertilisation by insects in nature. Sprengel discussed these five points in numerous honey-secreting flowers,

and succeeded in explaining most of their characters as contrivances for insect-fertilisation. His theory, although the first effort in this wide field, would have afforded a satisfactory key to the chief puzzles of the floral world had it not contained a very serious flaw, which Sprengel was not conscious of, and was therefore not in a position to remove. Since the conveyance of pollen to the stigma is obviously of no benefit to the insect, the same question should have arisen even from Sprengel's teleological standpoint, which nowadays comes up prominently when we consider his hypothesis from the standpoint of natural selection: "What advantage can it be to the plant that its pollen should be conveyed by insects to the stigma?" For just as according to our modern views only modifications which are of advantage to their possessor can be preserved by natural selection, so from the teleological standpoint only beneficial arrangements could be ascribed to the all-wise Creator. If the conveyance of pollen to the stigma by insects is of no greater advantage than the direct contact of the reproductive organs in the flower, then the preference of the former uncertain method to the latter seems unnecessary and capricious, and any theory based thereon falls to the ground.

It is remarkable in how many cases Sprengel recognised that the pollen is carried of necessity to the stigmas of *other* flowers by the insect-visitors, without suspecting that therein lies the value of insect-visits to the plant. In very many plants Sprengel had observed that the two sets of sexual organs in the same flower are not developed simultaneously; to this phenomenon he gave the name *dichogamy*. In his introduction (p. 43) he says expressly: "Since very many flowers are of one sex only, and probably as many more are dichogamous, nature seems to intend that no flower shall be fertilised by means of its own pollen," and as a proof of this he adduces an experiment performed by him on *Hemerocallis fulva*, which showed him that this plant is not fertile to its own pollen. So near was Sprengel to the distinct recognition of the fact that self-fertilisation leads to worse results than cross-fertilisation, and that all the arrangements which favour insect-visits are of value to the plant itself, simply because the insect-visitors effect cross-fertilisation!

But this omission was for several generations fatal to Sprengel's work, which was otherwise well fitted to give a powerful impulse to further research. For, both at the time and subsequently, botanists felt above all the weakness of his theory, and they set aside along with his defective ideas the rich store of his patient

and acute observations and his comprehensive and accurate interpretations.

Instead of the correlation of living organisms, which Sprengel had made the subject of observation and reflection with such admirable results, classification and afterwards anatomy and embryology occupied investigators so exclusively that no one ever thought of continuing Sprengel's beautiful researches or of testing their accuracy. His work remained forgotten until our ideas of organic nature were fundamentally changed by the progress of knowledge, and until the advantages of cross-fertilisation, which Sprengel only faintly realised, were recognised anew and more clearly through independent experiments.

The idea of independent creation of species, prevalent in Sprengel's time and so confidently stated in his book, was overthrown by progress in the three departments of classification, embryology, and paleontology; all three led consistently to the conception that the existing species of plants and animals must have originated from simpler forms; and Darwin's *Origin of Species* proved the point by demonstrating clearly and thoroughly how actual forces were operating before our eyes to modify living forms.

But, even before this great revolution in our conception of nature, one point which was needed to make Sprengel's theory efficient had been clearly perceived. A few years after Sprengel's book appeared, Andrew Knight (392), after some experiments on cross-fertilisation and self-fertilisation in the pea, laid down the law that in no plant does self-fertilisation occur for an unlimited number of generations. But his law received no further attention, and nobody conceived the idea of applying it in connection with Sprengel's theory. A like fate overtook Herbert (334), who summed up the result of his numerous experiments in this sentence: "I am inclined to think that I have derived advantage from impregnating the flower from which I wished to obtain seed with pollen from another individual of the same variety, or at least from another flower, rather than with its own" (p. 371). C. F. Gärtner (259) was led still more distinctly to the same result by experiments on *Passiflora*, *Lobelia*, and *Fuchsia*. Even when Darwin, in 1857 and 1858, published some new experiments on *Papilionaceæ* (151), which showed that the aid of insects or artificial imitation of their action was necessary for complete fertility, and that crossing of separate plants was actually to a great extent effected by insects, his re-enunciation of Knight's law remained ineffectual. The charm that had kept Sprengel's theories inoperative was only broken when,

in the next year, Darwin produced his *Origin of Species*, and in it emphasised Knight's law as a general law of nature, placing it on broader and surer foundations and uniting it intimately with his theory of natural selection. This theory showed for the first time the full value of Sprengel's work, and caused his book, which had been forgotten for seventy years, to play a prominent part in the investigation of the prime causes which determine the forms of flowers.

As a foundation for the hypothetic natural law that "no organic being fertilises itself for a perpetuity of generations, but that a cross with another individual is occasionally—perhaps at very long intervals—indispensable,"<sup>1</sup> Darwin showed that in all higher and the great majority of lower animals the sexes are separate, and that most hermaphrodite forms pair regularly; that, in the experience of breeders of animals and cultivators of plants, breeding in-and-in diminishes the strength and the productiveness of the offspring, while crossing with another breed, or with another stock of the same breed, increases both; that, according to the above-mentioned experiments of several botanists, the application of pollen to the pistil of the same flower is less efficient than pollen from another individual; that in very many plants the situation of the reproductive organs, exposed to the weather and often liable to injury, may be most simply explained if we admit the necessity of occasional crossing; that, according to his own experiments on *Papilionaceæ*, the exclusion of insect-visits in many cases diminishes or arrests productiveness; that, as Sprengel had shown in many cases and Darwin had confirmed, self-fertilisation is prevented in many flowers by the relative positions of the reproductive organs or by their ripening at different times; finally, that in no living organism do the structure or situation of the reproductive organs prevent occasional crossing with another individual of the same species. These statements, taken separately, were neither decisive nor free from objection, but collectively they lent a high degree of probability to Darwin's hypothesis; and so, from its close connection with the question of the origin of species and the fundamental importance that it therefore had for all botanical research, botanists could not help at once taking part for or against it, according to whether they were impelled by the general weight of evidence or deterred by the gaps in the chain.

The opposers justly maintained that though in the animal kingdom the possibility of occasional pairing might be admitted in

<sup>1</sup> *Origin of Species*, chap. iv. "On the Intercrossing of Individuals."

the case of the relatively few hermaphrodites which generally fertilise themselves, yet for the majority the common notion that the flowers are fertilised with their own pollen, either spontaneously or by the aid of insects or the wind, was as yet not disproved (cf. Treviranus, 742). They said justly that the observations quoted to prove the disadvantages of breeding in-and-in or of fertilising a flower with its own pollen were quite insufficient, and they called for more extended experiments. Finally, they pointed to the not rare occurrence of flowers which inevitably fertilise themselves, which even remain closed, and yet which are fully productive, as a difficulty in the way of Darwin's hypothesis not yet removed. From the nature of the case, complete proof seems impossible, either for or against this law; for neither, if it is true, can the necessity of occasional crossing be shown for all bi-sexual plants and animals; nor, if it is false, can any hermaphrodite which as a rule fertilises itself be kept under observation for an unlimited number of generations. But, since the facts which come within the scope of this law and by which its validity may be subjected to detailed proof are inexhaustibly numerous, continued research will either bring the probability of the law to the verge of certainty or make its improbability continually more conspicuous. And so the Knight-Darwin law was admirably fitted to lead to numerous investigations of phenomena hitherto left unobserved, and so to be highly valuable in furthering our knowledge, even if in the end its truth could not be universally and absolutely affirmed.

Darwin opened these new lines of investigation with his own incomparable researches. A few years after the publication of his *Origin of Species*, he showed by his wonderful book on orchids that he had by no means affirmed the general truth of Knight's law without having engaged in special researches himself. For he showed in this work that in almost all British orchids, and in all the foreign species within his reach, the flowers were adapted down to the most minute details for insect-visits, in such a way that insect-visitors could not fail to carry the pollen to the stigmas of other flowers. Only a few species in which self-fertilisation regularly took place formed an exception, as yet unexplained, to this general law; but since even in these cases the possibility of occasional crossing was not excluded, they formed no valid argument against the Knight-Darwin law.

This work, freed from the fundamental flaw of Sprengel's theory and permeated by Darwin's acute reasoning and observation, was a model for the study of the forms of flowers, and it gave

a powerful impetus to further research based upon Sprengel's work. Even Treviranus's well-founded objection that in most orchids, even our native species, the operation of insect-visitors was only concluded indirectly from the structure of the flowers and had not been directly observed, could not hinder this result of Darwin's book; on the contrary, it could only direct more general attention to the insects that actually performed the work of fertilisation. A paper published seven years later by Darwin (159), enumerating the insects observed to visit a large number of native orchids, shows to how great an extent attention had been attracted to this point.

Another line of investigation which Darwin initiated in the same masterly way, was the direct observation of differences between the action of pollen from the same and from another flower. It has been already mentioned that Sprengel instituted experiments on self-fertilisation in the case of *Hemerocallis fulva*, and that he recognised that the flowers of this plant were not fertile to their own pollen, and other instances of the same kind, or at least of diminished fertility upon self-fertilisation, had been accumulated by other botanists as has been already explained. Darwin collected these scattered facts and brought them under Knight's law which for the first time revealed their full significance, and at the same time he initiated a new method of research which placed the produce resulting from self-fertilisation alongside of the produce of cross-fertilisation in the struggle for existence, and so permitted the result of persistent self-fertilisation to be ascertained under natural conditions. In numerous plants which were found to be fertile with their own pollen, he fertilised some flowers with their own pollen and other flowers on the same plant with pollen from a neighbouring plant growing under the same conditions, excluding insects with great precautions; he allowed the resulting seeds to germinate on damp sand in the same vessel, and then planted them in pairs on opposite sides of the same pot; then, while all conceivable precautions were taken to keep both sides under the same conditions, he watched the growth of the plants to maturity. The same experiment was repeated with the seeds produced by these, and was continued from generation to generation.

In several cases (*Ipomœa purpurea*, *Mimulus luteus*), the plants resulting from cross-fertilisation showed even in the first generation a marked superiority over the others; they were larger in the proportion of four to three or even three to two, they flowered

Insects which visit the different kinds of flowers by turns in the same way, must, since the same parts of their bodies always touch organs at the same height in the flower, effect cross-fertilisation both in dimorphic and trimorphic plants in such a way that the stigma in one form of flower always receives pollen from anthers which stand at the same height in another form. Such crossing, which is the mode commonly occurring in nature and in which the size of the pollen-grain is always proportional to the length of the style that its tube has to traverse, was called by Darwin *legitimate*. In dimorphic heterostyled plants there are thus two ways in which legitimate fertilisation is possible, both occurring regularly in nature, viz., the fertilisation of long-styled flowers with the pollen of short-styled, and *vice versa*; similarly there are in such cases two kinds of illegitimate fertilisation, viz., long-styled flowers with the pollen of long-styled, and short-styled with the pollen of short-styled. In trimorphic heterostyled plants, on the other hand, six modes of legitimate cross-fertilisation are possible and occur regularly in nature; and there are twelve modes of illegitimate crossing, since each of the three kinds of stigmas is illegitimately fertilised if it receives pollen from either whorl of stamens in a flower of its own form or from one whorl of stamens in each of the other two. Now Darwin found, when he tried all the four modes of crossing in the dimorphic plants and all the eighteen modes in the trimorphic plants, and sowed the seeds from the resulting capsules and again crossed the offspring in various ways, that only the "legitimate" crossings resulted in full fertility, and produced normal and fully fertile offspring; while, on the other hand, illegitimate crossings led to all degrees of diminished fertility or even complete barrenness, and produced offspring which had all the characters of bastards produced by the union of distinct species.

The result of these investigations was particularly favourable to Knight's law, since it proved that in heterostyled plants not only the occasional crossing of separate flowers, but the regular crossing of separate individuals was absolutely essential for the maintenance of the species. At the same time it broke down the sharp boundary-line between Species and Variety which had formerly been supposed to be found in the more or less complete sterility of hybrids produced by crossing distinct species; and it showed, moreover, by the complete resemblance between the offspring of illegitimate unions in dimorphic and trimorphic plants and the bastard offspring of distinct species, that in the latter sterility both

at first and in the bastard offspring is not due to differences in the general structure, but exclusively to a difference in the action of the reproductive elements.

Attracted by Darwin's brilliant researches on heterostyled plants (1861-1868), many other investigators have since worked at the same subject. Darwin has collected their results, controlling them by his own observations and experiments and incorporating them with the results of his later investigations. His book contains all that we certainly know as yet concerning heterostyly, and treats also as comprehensively of polygamous, dioecious, and cleistogamic plants. It restricts the name *polygamous* to plants which possess male, female, and hermaphrodite flowers, and introduces the following new terms: *gynodioecious*, for plants which have hermaphrodite and also purely female individuals; *androdioecious*, for plants which consist of hermaphrodite and purely male individuals; *gynomonœcious*, for plants which have hermaphrodite and purely female flowers upon the same individual; *andromonœcious*, for plants in which one individual bears hermaphrodite and male flowers.

The most complete collection of all the known facts which contribute to prove Knight's law is given by Darwin in his work on the *Variation of Animals and Plants under Domestication*, in which he suggests many new and fruitful lines of research; but the three methods of investigation which Darwin originally used have been the chief aids in investigating the determining conditions of the forms of flowers. Numerous observers, among whom Friedrich Hildebrand, Federico Delpino, my brother Fritz Müller, and Severin Axell deserve special mention, have pushed forward along these new paths that Darwin opened; they have not only brought to light a mass of new facts, all tending to elucidate floral mechanisms on the basis of the Knight-Darwin law, but they have also disclosed many new general principles. These we may briefly review.

Hildebrand, in several laborious works, demonstrated that many floral contrivances which Sprengel had investigated, but had explained on the theory of self-fertilisation, were really adapted for regular cross-fertilisation; and he explained on the same principle, and in most cases figured, many forms that Sprengel had not examined. He extended the list of dimorphic and trimorphic plants, and applied Darwin's experiments to *Primula sinensis*, *Pulmonaria officinalis*, and several species of *Oxalis*; he also performed artificial self-fertilisation on these forms, and found that it led in general to even greater sterility than the illegitimate crossings. By his experiments on *Corydalis cava*, he showed that

self-fertilisation, which occurs spontaneously in all flowers of this plant, is completely inoperative, that even crossing of different flowers on the same individual gives a very poor yield, and that only the crossing of separate plants results in full productiveness. A powerful objection to the Knight-Darwin law was removed by this discovery. Finally, in his *Geschlechter-Vertheilung bei den Pflanzen* (1867), he has striven to show that throughout Phanerogams cross-fertilisation of separate individuals either takes place in all cases, or does so for the most part, or is at least possible; and he has given the following classification of phanerogamic flowers according to the completeness with which they exclude self-fertilisation:—

A. Male and female organs in different flowers (*dichlinism*).

Cross-fertilisation ensured, and effected by insects or by the wind. Ex. *Cannabis*.

B. Male and female organs in one and the same flower (*monoclinism*).

1. The organs of the two sexes not developed simultaneously (*dichogamy*).

(a) The male before the female.<sup>1</sup> Ex. *Geranium pratense*.

(b) The female before the male.<sup>2</sup> Ex. *Luzula pilosa*.

Self-fertilisation usually prevented, and cross-fertilisation effected by insects.

2. The organs of both sexes developed simultaneously (*homogamy*).

(a) Flowers expanding (*flores chasmogami*, Axell).

I. Anthers distant from the stigma.

a. Styles of different lengths on different plants of the same species (*Heterostyly*, Hild.; *dimorphism* and *trimorphism*, Darwin).

Self-fertilisation not altogether prevented, but either quite inoperative (*Pulmonaria officinalis*) or yielding little result (*Primula sinensis*).

β. Styles of the same length in all the flowers (*Homostyly*).

\* Reproductive organs changing their relative positions during the flowering period.

Self-fertilisation avoided, cross fertilisation effected by insects. Ex. *Anoda hastata*.

\*\* Reproductive organs remain unchanged in position during the flowering period.

† The aid of insects necessary for fertilisation.

Self-fertilisation to a great extent impossible, and cross-fertilisation necessary. Ex. *Orchidaceae*. Self-fertilisation

<sup>1</sup> Sprengel calls this species of dichogamy, *male-female*, or *dichogamia androgyna*; Hildebrand, *protandrous*; Delpino, *proterandrous*.

<sup>2</sup> Sprengel calls this species of dichogamy, *female-male*, or *dichogamia gynandra*; Hildebrand, *protogynous*; Delpino, *proterogynous*. Delpino distinguishes two varieties, viz., *proterogynia brachybiostigmatica*, where the stigmas are short-lived and wither before the anthers ripen; and *proterogynia macrobiostigmatica*, where the stigmas remain capable of fecundation until the anthers are mature, and where consequently self-fertilisation remains possible.

to a certain extent possible, but not necessary ; cross-fertilisation more probable. Ex. *Asclepiadeæ*.

†† The aid of insects not essential.

Self-fertilisation possible, but cross-fertilisation also effected by insects.

II. Anthers lying close to the stigma ; self-fertilisation inevitable.

\* No seed produced without cross-fertilisation, which is effected by insects. Ex. *Corydalis cava*.

\*\* Seed is produced on self-fertilisation, but cross fertilisation by insects is not excluded.

(b) The flowers never expand (*flores cleistogami*, Kuhn).

Only self-fertilisation occurs, and all cross-fertilisation is excluded ; but the plants have other flowers which open and are liable to cross-fertilisation. Ex. *Oxalis acetosella*.

Although the statements contained here with reference to the possibility of cross- or self-fertilisation have turned out not to be universally correct, and although the divisions merge into one another by many intermediate forms, as Hildebrand himself allowed, yet Hildebrand's scheme is very well adapted to serve as an artificial classification for the consideration of individual cases.

Delpino described the structure of very many flowers belonging to the most distant orders, showing them all to be adapted for cross-fertilisation. His descriptions are so clear and minute that he dispenses to a large extent with illustrations. In many cases he has directly observed the fertilising agents, and he states at least the families or genera to which they belong. He has shown that water as well as wind, and snails and honey-sucking birds as well as insects, play a part in the conveyance of pollen. He has shown in the most diverse instances how the form of the flower is determined by the special fertilising agent, and in several families (*Marcgraviaceæ*, *Marantaceæ*, *Artemisiaceæ*, &c.) he has made happy use of the gradual stages in adaptation to special fertilising agents in order to trace the mutual genetic relations of the members of the family. He has also shown strong evidence that in many cases the distributional area of a species is determined in the first instance by the presence of that animal which the flower has become adapted to be cross-fertilised by. And finally, choosing the various means of transport for the pollen as his basis of classification, and taking advantage ingeniously of the almost complete want of direct observations on the cross-fertilisation of Cryptogams, he evolved the following scheme of the whole vegetable kingdom, in all of whose members he also is of opinion that cross-fertilisation is either certain, or probable, or at least possible.

## I. Plants with Motile Reproductive Elements

(*Zoogamæ*).

Fucaceæ, Characeæ, Protonemeæ (Mosses and Liverworts), and Proembryonata (Ferns, Horse-tails, Rhizocarps, and Club-mosses), whose antherozoids, corresponding to the spermatozoids of animals, are endowed with spontaneous movement. Nearly allied to these are the Diatoms and Conjugatæ, in which the whole individual is motile.

## II. Plants which require External Aid to bring their Reproductive Elements together (*Diamesogamæ*).

- A. Plants fertilised by the agency of water (*hydrophilæ*).
- B. Plants fertilised by the wind (*anemophilæ*).
- C. Plants fertilised by the aid of small animals (*zooidiophilæ*).

### A. Plants Fertilised by the Agency of Water.

Delpino subdivides this class into two :—

1. Plants adapted for fertilisation under water. These require for cross-fertilisation that the stigma or the pollen-grains, or both, should be thin and filiform, and that the pollen should be abundant and of like specific gravity to the water (*Posidonia*, *Cymodocea*, *Zostera*, *Ceratophyllum*, *Florieæ*).

2. Plants adapted for fertilisation at the surface of the water. In these the pollen is specifically lighter than water, or is borne upon a floating raft; the peduncles of the female flowers elongate, sometimes aided by their spiral form, to bring the flowers to the surface of the water (*Ruppia*, *Vallisneria*).

### B. Plants Fertilised by the Wind.

The only positive character common to these is their smooth and easily scattered pollen; the negative characters common to them are absence of bright-coloured floral envelopes, of perfume, and of honey.

1. The Gymnosperms are all wind-fertilised, and are characterised by the absence of a stigma.

2. The anemophilous Angiosperms have for the most part enormously developed stigmas, which project in the form of long tails, brushes, laminæ, or discs; their male flowers are very seldom immovable, but are generally easily shaken by the wind, either the axis of the male inflorescence, or the peduncles of the male flowers,

or the filaments themselves, being long and pendulous; in some cases the stamens are explosive, and project all the pollen into the air. The following five varieties may be distinguished among anemophilous Angiosperms:—

(a) Forms with catkins, in which the axis of the male inflorescence is movable. Ex. *Corylus*, *Betula*.

(b) Forms with pendulous flowers. Ex. *Negundo fraxinifolium*, *Rumex*.

(c) Forms with long stamens. This is the most common variety, including almost all *Gramineæ*, *Cyperacæ*, *Juncaceæ*, *Cannabis*, *Humulus*, *Empetrum*, *Mercurialis*, *Ricinus*, *Plantago*, *Littorella*, *Callitriche*, *Myriophyllum*, *Hippuris*, the anemophilous species of *Thalictrum*, &c.

(d) Explosive forms. Ex. *Urtica*, *Parietaria*, *Morus*.

(e) Forms with immovable flowers. Ex. many Palms, *Potamogeton*, *Triglochin*, *Sparganium*, *Typha*.

### C. Plants Fertilised by Animals.

These usually possess bright colours or perfumes, and supply food to their fertilisers. The following classification has been supplied to me by Delpino, by letter:—

I. ORNITHOPHILÆ.—These plants are adapted for fertilisation by birds, which come in search either of honey or of small insects (*Trochilidæ*, *Nectarinia*, etc.). They present several different types. What is known concerning them is founded chiefly on the reports of travellers who were ignorant of the principles that should guide their investigation. Many of them possess large brilliantly-coloured flowers, very frequently scarlet, pouched in form, upright in position, and secreting great abundance of honey.

II. ENTOMOPHILÆ.—Plants whose flowers are adapted for fertilisation by insects. To this group belong all our native flowers which possess perfume or bright colours.

III. MALACOPHILÆ.—Plants whose flowers are adapted for fertilisation by snails. (These have as yet been observed by Delpino only.) The flowers are crowded so closely together, that the snails in creeping over them must come in contact both with pollen and stigmas. The plants are protected from the ravages of their voracious guests, either by secreting an acrid fluid which kills the snails (*Alocasia odora*), or by metamorphosis of the perianth into a thick fleshy tissue, with whose destruction the snails are content (*Rhodea japonica*).

In further subdividing entomophilous plants, Delpino omits all those plants which can be fertilised equally well by insects of various orders, and limits himself to forms which he considers to be adapted for particular insects. As such he distinguishes:—

1. *Melittophilæ*; plants adapted for fertilisation by (the larger) bees. These have diurnal flowers, with colours and scents attractive to man also, partly with concealed honey (*Salvia pratensis*), partly devoid of honey, and in that case with the pollen inclosed within the flower and only becoming apparent on special treatment (*Genista tinctoria*).

2. *Micromelittophilæ*; plants adapted for fertilisation by the smaller bees (and very many other small insects). These flowers possess quite incomprehensible attractions for their visitors, far more than in any other plants (*Herminium Monorchis*).

3. *Myiophilæ*; plants adapted for fertilisation by various Diptera. Their flowers present for the most part dull (yellowish, wine-red, speckled) colours, their odour is for the most part disagreeable both to man and to bees, and they display either an exposed surface of honey or else pollen only for their visitors (*Euonymus*).

4. *Micromyiophilæ*; plants adapted for fertilisation by minute Diptera. The flower or the inflorescence forms a chamber with a narrow entrance, often a temporary prison for the fertilising agents; honey is produced as a thin adhesive layer, or may be absent, in which case the pollen is abundant (*Aristolochia Clematitis*, *Arum*).

5. *Sapromyiophilæ*; plants adapted for fertilisation by carrion-flies and dung-flies. The flowers have a putrid smell, but the other characters of the group resemble those of the *Myiophilæ* (*Stapelia*, *Rafflesia*).

6. *Cantharophilæ*; plants adapted for fertilisation by beetles. These are large diurnal flowers of striking colours, affording convenient shelter, and containing an exceedingly large supply of pollen besides occasionally some easily accessible honey (*Magnolia*).

7. *Psychophilæ*; plants adapted for fertilisation by diurnal Lepidoptera. These have brightly-coloured diurnal flowers, whose honey is concealed at the base of a very narrow tube (*Dianthus*).

8. *Sphingophilæ*; plants adapted for fertilisation by Hawk-moths (Sphingidæ) and Noctuæ. These have light-coloured nocturnal flowers, with a strong sweet scent, whose honey is concealed at the base of a very long tube or spur (*Lonicera Caprifolium*, *Platanthera*).<sup>1</sup>

<sup>1</sup> Since the above was written, Delpino has completed his work, *Ulteriori osservazioni sulla dicogamia nel regno vegetale*, and in it the contrivances by which

My brother, Fritz Müller, has made many interesting observations on South Brazilian plants, in all the three lines of research which Darwin instituted. His results have been contributed partly to the *Jenaische Zeitschrift* and *Botanische Zeitung*, partly to Darwin's *Variation of Animals, etc.*, and are partly published for the first time in this book. He has found in the case of various orchids that they are not only sterile to their own pollen, but even that the pollen and stigma of the same flower act as fatal poisons to one another. In various flowers (*Chamissoa*, *Epidendrum*) he has discovered special contrivances in the act of being evolved, and especially in *Posoqueria* and *Faramaea* he has given clear proof that certain peculiarities, advantageous under the given conditions, have by no means attained their full perfection. The proof of this fact deserves special attention as a strong objection to the teleological theory. His comprehensive observations on Brazilian orchids will, it may be hoped, soon be published in a special work.

Severin Axell published in 1869 a book on the floral mechanisms of Phanerogams. It contains a clear historical review of the growth of our knowledge of the sexual relations of plants, and describes some new investigations of floral mechanisms and some experiments on the fertility of plants after self-fertilisation. It is remarkable for divesting of a certain onesidedness the conception that had

flowers are adapted for cross-fertilisation by animals are fully treated and very clearly arranged. He distinguishes :—

1. Adaptations which affect the senses of sight and smell in the fertilising agents.
  - (a) Colour.
  - (b) Scent.
2. Adaptations which affect the sense of taste : the attractions of pollen, honey, and other food-materials.
3. Arrangements which direct the actions of the fertilising agents, and make them more effective.
  - (a) Increase of conspicuousness by heliotropy, the position and grouping of the flowers, enlargement of particular organs, etc.
  - (b) The development of certain parts convenient for alighting on or standing on.
  - (c) Arrangements for preserving the nectar for the use of the fertilising agents.
  - (d) Arrangements for promoting the transfer of pollen from the anthers to the body of the fertilising agent, and thence to the stigmas.
  - (e) Arrangements for ensuring the transport of pollen from one flower to another, or from one individual plant to another.
  - (f) Arrangements for regulating the number of visits of the fertilising agents.
  - (g) Arrangements for adapting the flowers to particular fertilising agents.

Finally, Delpino gives a classification of flowers according to their different types, of which he distinguishes forty-seven, and he appends some remarks on the fertilising agents of plants and their habits.

become here and there prevalent of the significance of cross-fertilisation; and also for attempting to arrange all the floral mechanisms of Phanerogams in a series, according to their natural development from less perfect to more perfect forms.

The first impulse to the new investigation of flowers had been given by Darwin's notion of a general law that no organised being fertilises itself for an unlimited number of generations, or, as Darwin put it, that nature abhors perpetual self-fertilisation. And it was natural that those investigators who worked upon the lines laid down by Darwin should look upon the contrivances that were favourable to cross-fertilisation and unfavourable to self-fertilisation as so many proofs of the truth of Darwin's conjectural law. But they neglected to consider those flowers which frequently or regularly fertilise themselves; or, if such flowers forced themselves upon their notice, they were looked upon as isolated exceptions, and self-fertilisation was considered, in spite of them, as throughout injurious to plants. For instance, Hildebrand in 1867 says: "In most plants self-fertilisation is avoided by special contrivances or even rendered impossible, or if it does take place it is at least injurious;" and in 1869 he tries to prove "the law of the avoidance of self-fertilisation," and to treat as isolated exceptions *Calceolaria pinnata* and *Morina elegans*, in which he had found self-fertilisation to take place regularly when insect-visits fail. Similarly, in Delpino's writings until 1869 the idea recurs in many places, quite definitely, that "nature in general abhors self-fertilisation,"<sup>1</sup> while Darwin had only spoken of *perpetual* self-fertilisation. Now Axell justly showed that this conception entertained by Hildebrand and Delpino was unfounded, for he brought forward in opposition to it the facts that in many flowers self-fertilisation inevitably takes place in default of insect-visits, and that he himself had proved by experiment in many cases that such self-fertilisation results in the production of good seed; further, that many aquatic plants, which under ordinary circumstances expand their flowers at the surface of the water and are cross-fertilised by the wind or by insects, remain closed and submerged when the water is unusually high, and in such circumstances fertilise themselves and produce seeds which propagate the species; and finally, that many terrestrial plants, with irregular flowers which render self-fertilisation impossible, produce, instead of these or along with these, other flowers of simple structure

<sup>1</sup> For instance, in No. 177, p. 55, "L'antipatia che ha la natura per le nozze consanguinee" (1869).

which remain closed (*flores cleistogami*, Kuhn) and produce seed regularly by self-fertilisation. He supposed that the existence of cleistogamic flowers was due partly (e.g. *Lamium amplexicaule*) to low temperature, which hindered the development of the ordinary flowers, and partly to failure of the insects which under normal circumstances effected cross-fertilisation.

By this explanation, Axell rectified the conception that was so distinctly uttered by Hildebrand and Delpino in their earlier writings, viz., that cross-fertilisation is advantageous and self-fertilisation disadvantageous for plants, by showing that though cross-fertilisation is better than self-fertilisation, yet self-fertilisation is infinitely better than absence of fertilisation and consequent



FIG. 2.—Cleistogamic and ordinary flowers of *Lamium amplexicaule*.

1—4, large ordinary flower, not quite twice natural size. 1, entire flower; 2, oblique view of mouth, showing anthers and stigma; 3, upper part of corolla just before the flower opens; 4, nectary (n) and ovary (ov).

5—10, small cleistogamic flower (5-8,  $\times 5$ ; 9, 10,  $\times 24$ ). 5, entire cleistogamic flower from the outer side; 6, corolla, opened by force, seen from the side; 7, the same, opened less widely, seen from below; 8, corolla of a cleistogamic flower, unopened, from below; 9, essential organs of a cleistogamic flower undergoing self-fertilisation, two stamens having been removed; 10, ovary and nectary seen from the front and right.

sterility; and he also removed by his elucidation of cleistogamic flowers one great objection to the Knight-Darwin law,—the argument which was used against it by H. von Mohl.

Axell founds his attempt to classify all floral mechanisms of Phanerogams in the natural order of their development upon two laws which he lays down as axioms: (1) Nature strives to increase as much as possible the number of individuals in each species; and (2) she strives to attain the greatest possible results by the simplest possible means. If, instead of abiding by the teleological standpoint which personifies nature, Axell had risen to the objective conception of nature which Darwin founded, he might

have stated these two laws somewhat as follows: (1) every species of animal and plant has, in otherwise similar circumstances, the greater prospect of survival in the struggle for existence, the more numerous the offspring that it leaves; (2) every individual may, under otherwise similar conditions, be preserved the more easily in the struggle for existence, the simpler its requirements are. He would not then have required to state these laws as axioms, for they are seen to be immediate consequences of the theory of natural selection. Starting from these two laws, Axell saw in every economy of material, space, or time, an improvement in the mechanism of the flower. Accordingly he considers the arrangement in anemophilous flowers the most primitive and most imperfect form amongst Phanerogams, since it necessitates an immense waste of pollen, which is avoided in cross-fertilisation by insects. In both the anemophilous and the entomophilous sections, Axell recognises a further advance in the transition from diœcious to monœcious and monoclinic forms, since in this arrangement there is not only increased economy of material (floral envelopes, pollen), but increasing certainty of sexual reproduction. In the group of monoclinic entomophilous flowers, Axell considers that a further advance is shown in passing from dichogamic to *herkogamic* flowers (those in which self-fertilisation is hindered by the relative positions of the parts), and from these to the heterostylic (dimorphic and trimorphic), and finally from these to the homostylic plants with irregular flowers and again to those with regular flowers.

According to Axell, the forms which stand nearest to the diclinic entomophilous flowers are the dichogamic,<sup>1</sup> as in both of these types two insect-visits are necessary for each act of fertilisation, and many insect-visits which are paid successively to flowers in the same stage of development remain useless to the plant. Among homogamic entomophilous flowers, the *herkogamic*, in Axell's opinion, share with the dichogamic forms the disadvantage of not being able to fertilise themselves in case of need; but they stand one stage higher, since each act of fertilisation requires only a single insect-visit. This is also the case in heterostylic forms, which according to Axell stand yet a stage higher, since in them self-fertilisation, though very difficult, is not impossible. Finally,

<sup>1</sup> Axell allows the quite unfounded supposition that the corolla begins to wither and the secretion of honey ceases as soon as pollen is applied to the stigma to lead him into the equally erroneous conclusion that proterandrous dichogamy only is possible in entomophilous flowers; and this conclusion leads him to doubt the accuracy of many observations which are opposed to his view.

among homostylic forms, in which the possibility of self-fertilisation is unchecked, those with regular flowers stand, according to Axell, on a higher grade than those with irregular flowers, since they permit the visits of more various insects. Axell thus arrives at the following order of development:—

- A. Flowers which are fertilised by the aid of an extraneous medium of transport (*flores chasmogamæ*).
  - I. Anemophilous forms: (a) dicæcious, (b) monæcious, (c) dichogamic (proterogynous), (d) homogamic.
  - II. Entomophilous forms:
    - a. Self-fertilisation hindered by
      - 1. Diclinism } Two insect-visits necessary for each
      - 2. Dichogamy } act of fertilisation.
      - 3. Herkogamy . . . . . } Only one insect-visit
    - b. Self-fertilisation not hindered. } necessary for each
      - 1. Heterostyly. 2. Homostyly } act of fertilisation.
- B. Flowers which fertilise themselves without the aid of an extraneous medium of transport (*flores cleistogamæ*).

If we review the lines of research above described, in order to get a clear idea of which path leads us most surely to the conditions determining the forms of flowers, it becomes plain that two different aims must be kept in view; these are closely connected, and sometimes within certain limits mutually depend upon one another, but they cannot be confounded without danger; viz. (1) the elucidation of floral mechanisms, and (2) the proof of the Knight-Darwin law.

Sprengel kept in view as the sole aim of his researches the explanation of the characters of flowers on certain presumptions which were to be justified by the constant possibility of such explanations; and his results were singularly fortunate so far as was possible with his teleological conceptions, and without knowledge or foreshadowing of the advantage of cross-fertilisation. Darwin remedied both flaws in Sprengel's theory, since he not only gave complete expression by his theory of natural selection to the new conceptions that had gradually grown up, but he also made the definite statement, and took steps to prove it, that the effect of cross-fertilisation is advantageous. But he did not content himself with the statement that cross-fertilisation leads to a more vigorous offspring than self-fertilisation, which would have sufficed provisionally to explain the contrivances in flowers, but he laid down

But while we must, on the one hand, strive to limit our assumptions as much as possible, in order to keep a basis fully demonstrable by experiment for our conclusions, we must, on the other hand, that these conclusions may rest firm, demand the securest possible establishment of all accessible facts which can influence the mutual relations between flowers and the agents which fertilise them.

Of the various fertilising agents, wind and water are so simple and regular in their action that it is easy to review the circumstances of the case, and to recognise how the comparatively simple contrivances in anemophilous and hydrophilous plants are determined by the nature of the medium of transport. But the insects<sup>1</sup> which act as carriers of pollen are so various in size, form, length of proboscis, food-material, mode of movement, colour-sense, &c., their abundance depends on so many conditions, and their visits to particular flowers are so influenced by weather, the competition of other insects, the attractions of other neighbouring flowers, &c., that the mere investigation of floral contrivances, and the mere general establishment of the fact that certain flowers are actually visited and fertilised by insects, can never lead to a perception of the primitive conditions which determine any specific peculiarity in a flower. Only when it is accurately ascertained for many and various flowers of the same neighbourhood by what insects and how abundantly by each each species is visited, what in each case each visitor comes in search of, how each acts in its visits, how the dimensions of their bodies correspond to the dimensions of the flowers (for instance, the length of their proboscis to the length of the tube and spur), what parts of their bodies come in contact with the pollen and the stigma, and so forth; when further, for each of these flowers, not only the form, arrangement, and order of development of the separate parts, but also the area of conspicuous surfaces, the diameter of the entrance, the depth of the tube in which the honey lies, in short every point which can affect the insect-visitor, has been accurately ascertained—then only may we hope, by comparing the characters of flowers and their insect-visitors, to attain to accurate knowledge instead of the mere surmises concerning the conditions that primitively determine any floral character.

It is plain that in such facts all previous investigations have left wide gaps. Even Delpino, who paid more attention than any

<sup>1</sup> Snails and birds may be left out of the question, as they do not play an important part in fertilising any native plants.

previous observer to the insect-visitors, based his generalisations upon far too few observations of insect-visits; both his classification of entomophilous flowers<sup>1</sup> and his general conclusions concerning the fertilisers of whole families (*Compositæ*, *Boraginæ*, &c.) require essential modification. In no single case do the observations hitherto made on anthophilous insects suffice either to explain the differences between nearly allied species of flowers or to settle the primitive conditions determining any specific floral character.

In order to attain to substantial knowledge concerning such determining conditions, we must modify in two respects the modes of investigation hitherto adopted, based upon the Knight-Darwin law :—

(1) Instead of considering those flowers in which cross-fertilisation in case of insect-visitors is distinctly insured or in which self-fertilisation is distinctly opposed, we must look upon all entomophilous flowers without exception as requiring elucidation to the same degree; and in each species we must consider the possible or inevitable occurrence of self-fertilisation in absence of insects with as much care as the certainty or possibility of cross-fertilisation in case of insect-visits.

(2) Instead of confining ourselves to the investigation of floral mechanisms or of at most ascertaining in a general way by what groups of insects a particular plant is visited and cross-fertilised, we must consider the insect-visitors with as much care as the flowers visited by them. We must compile for each species of flower a list as complete as possible of its visitors, in order to come by wide comparison to a safe conclusion regarding what effect peculiarities in colour, odour, the secretion and concealment of the honey, etc., have upon insect-visits, and so upon the fertilisation of the plant. We must also take note of the way in which the insects are fitted to obtain their floral diet, and we must try to trace the gradual evolution of such adaptations through all stages, since many characters of flowers and of their visitors (*e.g.* length of tube and length of proboscis) have been developed in reciprocal adaptation, and can therefore only be understood when considered together.

This is the path which I have sought to enter on in the present book. How far I have succeeded in my task is for others to decide. To permit of fair judgment, I must myself explain certain omissions in my work.

<sup>1</sup> *Supra*. p. 15.

I have been unable to pay equal attention to all groups of anthophilous insects. I could neither determine by myself the minute flies and gnats, ichneumon-flies and their allies, aphides and species of *Meligethes* and *Thrips*, nor could I get them reliably determined by others; these, accordingly, along with most ants and some saw-flies, are referred to only in general terms. Nocturnal lepidoptera and microlepidoptera are left almost untouched for another reason, viz., the difficulty of observing them upon flowers in the dim light. On the other hand, I have paid close attention to the beetles, the larger flies, bees, wasps, and butterflies, and I have determined their species with the aid of the entomologists referred to in my preface. But just on account of this simultaneous observation of so many insect groups, in the case of the most frequented flowers it is probably only the commonest species that have fallen into my hands; so that it will be easy for any collector of a special group to show the most extensive omissions in my richest lists. I indeed hope that this may be done on the largest scale.

In hastening to publish provisionally an account of my researches, it was further impossible for me to follow out thoroughly in the case of all the groups of anthophilous insects the modifications which fit them for a floral diet, and to prove that such modifications have been evolved gradually. In the case of bees, the most important visitors of flowers, I have attempted to give such proof in a special work. In the present book I must limit myself to giving a general account of the adaptations of insects to the flowers visited by them, so far only as seems essential for a right understanding of the actions of insects upon flowers.

#### NOTES ON THE HISTORICAL INTRODUCTION.

1. Severin Axell gives in his work (17), published in 1869, a short review of the development of our knowledge of the sexual relations of plants. He says :—

“Although we meet even in ancient Greek and Roman authors with dim foreshadowings of the sexuality of some diclinic plants, it is only towards the end of the seventeenth century that we find the existence of two sexes in the higher plants clearly and generally acknowledged. In 1682, Nehemias Grew published his book *The Anatomy of Plants*, in which he maintained the necessity for the pollen to act upon the pistil to form the fruit. Rud. Jac. Camerarius<sup>1</sup> and Sebastian Vaillant<sup>2</sup> strongly supported the new views, partly

<sup>1</sup> *Epistola de sexu plantarum* (Tübingen : 1694).

<sup>2</sup> *Discours sur la structure des fleurs, etc.* (Paris : 1717).

by experiment, partly by specifying the sexual organs in various forms of flowers; while on the other hand Tournefort<sup>1</sup> and Pontedera<sup>2</sup> tried to prove that these views were untenable, chiefly from philosophical considerations. The contest may be considered to have been settled in its main point by the masterly collection of proofs of the sexuality of plants given by Linnæus in 1735.<sup>3</sup>

After it had been shown that pollination is an essential condition for the production of seed, it still remained to show how the pollen-grains are conveyed to the stigma; and attempts were made to elucidate this also, but with less success. It was of course seen that in diclinic plants some external agency must convey the pollen-grains from the male to the female flowers, and the whole effect was ascribed to the wind; in hermaphrodite flowers, on the other hand, it was supposed that the stigma is dusted with pollen from the same flower without the cooperation of any external agency. This had to take place either by the anthers and stigma coming in contact, or by the pollen falling down upon the stigma: the former would have to take place either before the flower opened, or by movements of the reproductive organs<sup>4</sup>; to explain the latter, it was laid down as a general rule that those flowers whose stamens overtop the style have an erect position, and that those in which the style overtops the stamens are pendulous.<sup>5</sup> Meanwhile, since it was observed that many flowers contain honey and are visited by insects, the idea arose that these must be of some use in fertilisation. It was, however, supposed that in their visits they simply shake pollen from the anthers,<sup>6</sup> and not that they carry pollen from one flower to another. The importance and in many cases the necessity of the action of insects was not at all recognised,<sup>7</sup> either in general or in any single case, if we except the observation of the fertilisation of *Ficus carica* by *Chalcis Psenes* (*Ficus* in *Amen. Acad. i.*).

This last observation stood for a long time isolated, until in 1761 Joseph Gottlieb Koelreuter demonstrated the necessity of insects' aid in several other cases, such as *Cucurbitaceæ*, *Irideæ*, *Sambucus*, and *Viscum*.<sup>8</sup> This illustrious man remarked also, that in *Mulvaceæ*, *Epilobium*, and *Polemonium* (*Vorläuf. Nachr.* p. 34), self-fertilisation is prevented by maturation of the reproductive organs at different times, and that in these plants the pistil of an older flower is fertilised by the aid of insects with pollen from a younger flower.<sup>9</sup> In the case of most plants, however, he held to the old

<sup>1</sup> *Institutiones rei herbariæ* (Paris: 1700).

<sup>2</sup> *Anthologia, seu de floribus naturæ* (Patav.: 1720).

<sup>3</sup> *Fundamenta botanica* (Amsterdam: 1735).

<sup>4</sup> It was Vaillant who first observed this phenomenon. For the meaning which was assigned to it, see Linnæus, *De nuptiis et sexu plantarum*, 1729, first printed in 1829; and "*Sponsalia Plantarum*," p. 46, in *Amenitates Academicae*, i.

<sup>5</sup> Linnæus, *loc. cit.* and "*De œconomia Naturæ*," in *Amen. Acad. i.*

<sup>6</sup> "*Sponsalia Plantarum*" and "*De neclariis floribus*," *Amen. Acad. iv.*

<sup>7</sup> See, for instance, the explanation of the act of fertilisation in *Viola tricolor* in "*Sponsalia Plantarum*," p. 87.

<sup>8</sup> *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen* (Leipzig: 1761), and *Fortsetzung der vorläufigen Nachricht* (Leipzig: 1763).

<sup>9</sup> After showing how well the organisation of these plants is fitted for crossing Koelreuter remarks: "An id aliquid in recessu habeat, quod hujusmodi flores nunquam proprio suo pulvere, sed semper eo aliarum sue speciei impregnentur merito quaeritur. Certe natura nil facit frustra."

explanation of fertilisation, which, erroneous as it was, was not controverted until the appearance of Sprengel's book and, afterwards still more thoroughly by F. J. Schelver<sup>1</sup> and August Henschel.<sup>2</sup> The researches of these botanists showed clearly that in most plants pollination of the pistil is impossible or at least improbable without the cooperation of some external agent. The last two authors, since they did not ascribe the proper importance to insect-visits, were led into the error of denying the sexuality of plants. On the other hand, Sprengel has not only rendered the negative service of showing, as the others did, how the prevalent conception of the mode of fertilisation is directly contrary to the actual relations, but also the positive service of removing the last objection to the sexual theory by his theory of the adaptation of flowers to fertilisation by insects.<sup>3</sup>

2. Even Sprengel notes several instances of incomplete adaptation; e.g. on page 259, "Although the flowers (*Lychnis dioica*) being nocturnal are not adapted for humble-bees, yet these make use of their nectar."

3. Perhaps F. G. Kurr has reviewed most thoroughly Sprengel's observations in his book *Untersuchungen über die Bedeutung der Nektarien in den Blumen*, which is replete with his own observations and ideas. But even this acute observer<sup>4</sup> lets us clearly trace how his ignorance of the advantage of cross-fertilisation prevented him from agreeing with Sprengel's explanations, and how, along with Sprengel's theories, he rejected his correct observations (e.g. in the case of *Campanula*) in order to cling to old errors.

Severin Axell, in his above-mentioned work, cites the following later botanists who rejected Sprengel's discoveries; "Treviranus,<sup>5</sup> in upholding the sexuality of plants against Henschel, denies altogether that the organs of the two sexes mature at different times, and declares that the pollen and the stigma always ripen simultaneously; Schultz-Schultzenstein<sup>6</sup> attacks Sprengel, and charges him with false statements; De Candolle<sup>7</sup> asserts: 'M. Conrad Sprengel a cherché à développer ses idées, plus fondées, je le crains, sur des théories métaphysiques que sur la simple observation des faits;' Mikán criticises him for his description of the apparatus for fertilisation in the violet; even Robert Caspary says, 'quod censeo, non injuste dici potest, inter omnes illas Sprengelii observationes, quas certissimas profert, quo modo insecta flores fecundent, ne unam quidam esse, ex qua certe concludi possit, nullo alio modo flores fecundari quam auxiliis insectorum.' Robert Brown alone, in his well-known paper (114) on the fertilisation of *Asclepiadaceæ* and *Orchidaceæ*, confirmed the accuracy of Sprengel's statement that the aid of insects is necessary for the fertilisation of these plants, although he, like Sprengel, failed to notice that here cross-fertilisation occurs and not self-fertilisation."

Just as, according to these extracts, most botanists reviewed onesidedly the weakness of Sprengel's theory, and threw overboard the good along with the defective; so, with equal onesidedness, Delpino and Severin Axell have

<sup>1</sup> *Kritik der Lehre von den Geschlechtern der Pflanzen* (Heidelberg: 1812).

<sup>2</sup> *Von der Sexualität* (Breslau: 1820).

<sup>3</sup> Cf. Severin Axell, "Om det färgade hyllets betydelse för växten," *Bot. Notiser* Tredje häftet, 1868.

<sup>4</sup> *Loc. cit.* pp. 138, 139.

<sup>5</sup> *Die Lehre vom Geschlechte der Pflanzen* (Bremen: 1822).

<sup>6</sup> *Die Fortpflanzung und Ernährung der Pflanzen* (1828).

<sup>7</sup> *Organographie végétale*, i. p. 538 (Paris: 1827).

raised up Sprengel's work too high, and have passed over in silence the flaw which explains why it remained inoperative for so many generations. Delpino<sup>1</sup> says in regard to the neglect of Sprengel,—and Severin Axell agrees with him: "It is sad to witness this war of error against truth, especially when the contest was begun by one who lived subsequently, and who, instead of profiting by the truths discovered by his predecessor, only set to work foolishly to deny them." While fully acknowledging the justice of this opinion, I think that, to be fair to both sides, we must add: Sprengel's discovery is an instructive example of how even work that is rich in acute observation and happy interpretations may remain inoperative if the idea at its foundation is defective.

4. Darwin says in his paper on the fertilisation of Papilionaceous flowers by bees (p. 461): "Andrew Knight many years ago propounded the doctrine that no plant self-fertilises itself for a perpetuity of generations. After pretty close investigation of the subject, I am strongly inclined to believe that this is a law of nature throughout the vegetable and animal kingdoms." As Darwin also mentions, Knight had found by experiment in the case of the Pea that more numerous seeds and more vigorous offspring are obtained by the application of pollen from another flower than by self-fertilisation.

<sup>1</sup> *Sull opera "La distribuzione dei sessi, etc." del Prof. F. Hildebrand, p. 10.*

## PART II.

### THE INSECTS WHICH VISIT FLOWERS.

OUR native flowers are visited by examples of all the main divisions of insects; but these divisions differ greatly in regard to the number of their anthophilous species, the extent to which these restrict themselves to flowers for their food, their relative importance in fertilisation, and their special adaptations for the work. And though, as a general rule, the degree to which a group of insects is adapted structurally for a floral diet is proportional to their importance as fertilisers, this does not hold good always. In the following sketch, our insect-groups are arranged according to their progressive adaptations for obtaining food in flowers.

#### Orthoptera and Neuroptera.

These groups contain, at least among our native species, no form which is habitually anthophilous, or which shows any trace of adaptation for a floral diet.

Earwigs (*Forficula auricularia*, L.) often creep in the daytime into flowers (*Campanula*, *Papaver*, *Tropæolum*, roses, pinks, peonies, etc.), whose softer parts they feed upon at night. Grasshoppers leap or fly on to various parts of plants, and so occasionally on to the flowers, to feed.<sup>1</sup>

I have seen a small dragon-fly (*Agrion*) settle repeatedly on flowers of *Spiræa*, apparently only to sun itself.

I have so often seen species of *Hemerobius*, *Sialis lutaria*, L., and *Panorpa communis*, L., upon flowers of Umbelliferæ, and

<sup>1</sup> Delpino once found a small green grasshopper on flowers of *Ophrys aranifera* (172). Darwin states, on the authority of Mr. Swale, that in New Zealand several species of grasshoppers have been observed to fertilise papilionaceous plants (152, p. 451). This seems to me almost incredible. In South Brazil my brother Fritz Müller has found a *Pseudomops*, probably *P. laticornis* (Perty), common on flowers.

watched them bending their heads down on to the honey-secreting disc, that I could not doubt that they were feeding there. In the summer of 1855, I took *Ascalaphus macaronius* on flowers of Umbellifers in meadows at Laibach.

The case of *Panorpa communis*<sup>1</sup> is quite clear, for it even visits flowers with more deeply-seated honey (Rosaceæ, Compositæ, e.g. *Eupatorium cannabinum*), plunging its long beak-shaped head into the tubes. One might be inclined to look upon this elongated head as specially adapted for the quest of honey, were it not that the little wingless, closely-allied *Boreus hiemalis*, which never visits flowers, but lives among moss,<sup>2</sup> shows the same peculiarity.

It is also exceptional for Neuroptera to visit flowers. They are more abundant than the above-named Orthoptera, and occasionally cross-fertilisation may be effected by them; but certainly no native flower has been modified by the agency of either group.

### Hemiptera.

In their importance as fertilisers, Hemiptera stand higher than the preceding divisions, for in one group, the bugs (*Hemiptera heteroptera*, Latr.), several forms are habitually anthophilous; whether they possess corresponding adaptations for a floral diet is still uncertain.

The species of *Anthocoris* (so called from their fondness for flowers) are fitted by their small size to creep into and suck honey from very various flowers. I have taken several undetermined species of *Capsidæ* and *Anthocoridæ* on flowers of Umbelliferæ, Compositæ, and *Salix*, seeking honey and dusted with pollen, I found *Tetyra nigrolineata* abundantly on flowers of *Daucus Carota* in Thuringia, and I have seen *Pyrocoris aptera*, in spring, thrusting its proboscis (about four mm. long) into florets of the dandelion; the underside of its legs and body was dusted with pollen, and it seemed to be a regular and efficient fertiliser. I have seen no structural adaptations for floral visits in any of these insects, unless the small size of *Anthocoris* be of this nature; the long proboscis is found in many allied forms which never visit flowers. No flower has been shown to be specially adapted for the visits of field-bugs, and I know no species for whose fertilisation these insects are especially important. The structure of their proboscis need not be considered.

<sup>1</sup> *Panorpa communis* is habitually carnivorous.

<sup>2</sup> I have found *Boreus hiemalis* repeatedly among moss on the Lichtenauer mountain, near Willebadessen, but only in the middle of winter.

### Coleoptera.

In contrast to the foregoing groups, Coleoptera afford unequivocal adaptations to a floral diet. They are of far greater importance as fertilisers, for many species in widely different families feed at times on flowers, and a still greater number confine themselves to such food exclusively. None of our native plants are fertilised exclusively or even mainly by Coleoptera; but the large genus *Meligethes* alone, the species of which are small and can creep into most flowers, is of more importance as a fertilising agent than all the preceding groups taken together. On the other hand, beetles do great harm to many flowers by nibbling their reproductive organs.

In flowers where the honey lies fully exposed (*Umbelliferae*, *Cornus*, *Parnassia*), many species of beetles may be seen licking it; and in flowers with exserted stamens and with the honey concealed though accessible to short-lipped insects (*Rosiflorae*, *Compositae*), beetles may be seen licking up honey, devouring pollen or even the whole anther, or nibbling at the petals and stamens. In flowers which have conspicuous anthers but which secrete no honey, or where the honey lies too deeply hidden, (*Ranunculaceae*, *Plantago*), the beetles feed upon the pollen, the anthers, and other soft parts of the flower. Besides these, flowers which afford shelter from wind and rain (*Campanula*, *Digitalis*) are visited by beetles, which then feed upon the pollen and the soft tissues. In warmer countries, according to Delpino (178, I., p. 234), several flowers of this kind, *e.g.* *Magnolia*, have become adapted for fertilisation by beetles (*Cetonia*) exclusively. Lastly, we sometimes find beetles upon flowers which seem to offer none of the advantages above described, but only allure by means of their bright colours; thus, for instance, *Cryptoccephalus sericeus* and *C. Moravi* are often attracted by the bright yellow flowers of *Genista tinctoria*.

A review of the mode of life of insects which visit flowers, and of the families to which they belong, shows continuous gradations from those which never visit flowers to those which seek them as a secondary matter, and finally to those which entirely depend upon them. This shows clearly that insects which originally did not avail themselves of flowers gradually became more and more habituated to a floral diet, and only

became correspondingly modified in structure when they had learned to depend upon such a diet exclusively: so that the view (defended by Delpino), according to which certain flowers have been predestined for certain insects, and *vice versâ*, is untenable.<sup>1</sup>

In the larval state I have observed only one anthophilous beetle (*Helodes arcta*) to affect a floral diet; other beetles, which as larvæ feed on the parts of flowers, *e.g.* the Apple Gouger (*Anthonomus pomorum*), abandon flowers on attaining to the perfect state. The larvæ of beetles which are anthophilous when mature, are partly carnivorous (*Telephorus*, *Trichodes*, *Coccinella*), partly feeders on putrid animal matter (*Dermestidæ*), partly feeders on living or decaying vegetable matter (*Buprestidæ*, *Cerambycidæ*, *Elateridæ*, *Chrysomelidæ*, *Curculionidæ*, *Cistela*, *Lagria*, *Mordellidæ*, *Lamellicornia*).

Of the carnivorous larvæ, most species of *Coccinella* and *Telephorus* remain carnivorous in the perfect state, but some (*Coccinella septempunctata*, *C. 14punctata*, *C. mutabilis*, *Telephorus fuscus*, *T. melanurus*, etc.) though they do not disdain flesh altogether resort more or less to flowers, and *Trichodis* in the perfect state restricts itself absolutely to a floral diet.

In the next group, larvæ which feed upon putrefying animal matter, *Dermestes* retains the same habit in its perfect state, never visiting flowers, and *Anthrenus* and *Attagenus* sometimes do the same; but of these latter genera, the same species which under favourable circumstances, *e.g.* in neglected zoological collections, feed for many generations on animal matter, without ever leaving the cases whose contents they are destroying, in other circumstances may be found by hundreds upon flowers, busily feeding upon pollen and honey.

The most perfect gradations are exhibited, however, by those families whose larvæ feed upon vegetable matter, as the following selection shows: I have taken no species of *Bostrichidæ* on flowers; of the *Curculionidæ*, only a tiny part of the family resort (and then exceptionally) to flowers, whether of the same plants in which they pass their earlier stages (*Gymnetron campanulæ*, *Larinus Jaceæ* and *senilis*),<sup>2</sup> or of other plants on which they find freely accessible honey (*e.g.* *Otiorynchus picipes* on *Cornus*, species of *Apion* on *Adoxa* and *Chrysosplenium*); the *Chrysomelidæ*,

<sup>1</sup> Cf. the discussion of Delpino's teleological conceptions in the fourth section.

<sup>2</sup> I have found larvæ and pupæ of *Larinus senilis*, F., at Mühlberg in Thuringia, at the base of the capitula of *Carlina acaulis*, and the perfect insect on the leaves and now and then on the flowers of the same plant.

developed to insure greater success in the search after food;<sup>1</sup> and we can distinguish how a dependence on flowers has sprung up at different epochs of time, for in some beetles there has been time for the attainment of adaptations, and then for their divergence to form genera and families; while others, which have acquired the habit later, remain isolated anthophilous species among near allies which never resort to flowers.<sup>2</sup>

### Diptera and Thysanoptera.

The Diptera stand on a higher grade than the Coleoptera in the matter of adaptation to a floral diet, and are of far more importance for fertilisation. While only a small fraction out of all the species of Coleoptera resort to flowers, probably the majority of the Diptera do so. While, further, the mouth-organs of our native beetles show only commencing adaptations, which extend at most over small families, and may be easily traced by intermediate stages to their origin, in flies and gnats the mouth is so deeply modified that it is exceedingly difficult to trace back its parts to the primitive form of the original biting insect-mouth.<sup>3</sup> For our present purpose it will suffice to discuss the structure of the mouth-organs and the manner of using them in those Diptera which are specially important as fertilisers of our native flowers, without entering into questions of phylogeny.

The family of the Drone-flies, etc. (*Syrphidae*), are alone of far more importance as fertilisers than all our other Diptera put together. Most of their numerous and often very common species depend mainly or exclusively on a floral diet, and in this family are found the most perfect adaptations to a diet alternately of pollen and honey. Accordingly, to illustrate the mouth-organs of flies, I

<sup>1</sup> I have fully discussed the development of a dependence on flowers in beetles in a special work. This treats of the first transition to a floral diet; the progress towards entire dependence on honey and pollen; the attainment through practice of a certain ease of action upon flowers, and its hereditary transmission; and the similar behaviour of different beetles which have acquired equal degrees of structural adaptation (H. Müller, "*Die Entwicklung der Blumenthätigkeit der Insekten*," *Kosmos*, Bd. ix. pp. 258-272).

<sup>2</sup> The above refers only to our indigenous forms. Tropical and subtropical beetles show far more striking adaptations to a floral diet. For instance, in a *Nemognatha* which my brother Fritz Müller observed sucking flowers of *Convolvulus* at Itajahy and sent to me, the maxillæ are transformed into two sharp grooved bristles 12 mm. long, which when opposed form a tube like the proboscis of a butterfly, but of course not capable of being rolled up (cf. H. Müller, "*Ein Käfer mit Schmetterlingerrüssel*," *Kosmos*, Bd. vi. pp. 302-304; Hagen, *Proc. of the Boston Soc. of Nat. Hist.* vol. xx. pp. 429, 430, 1880; H. Müller, *Kosmos*, Bd. x. p. 56).

<sup>3</sup> I have explained my view of the descent of Diptera from *Phryganida* in a paper entitled "*Anwendung der Darwin'schen Lehre auf Blumen und blumenbesuchende Insekten*," *Verh. der Naturh. Ver. für pr. Rheinl. u. Westf.* 1869.

take the most specialised and most abundant of the *Syrphidæ*, *Eristalis* and *Rhingia*.

In *Eristalis* the outstretched proboscis is seen to be composed of three segments (Fig. 4, 4, 5, 6, and Fig. 5, 1): (1) the membranous basal piece (*g*), which bears anteriorly two unpaired (*h*, *i*) and two paired (*k k*) elongated chitinous pieces, and external to the latter two palps (*l l*); (2) the membranous and very contractile middle segment (*f*), only clearly separated on the lower surface; and (3) the extremity of the proboscis, supported beneath by a stiff chitinous plate (*c*), and bearing at its apex two contiguous

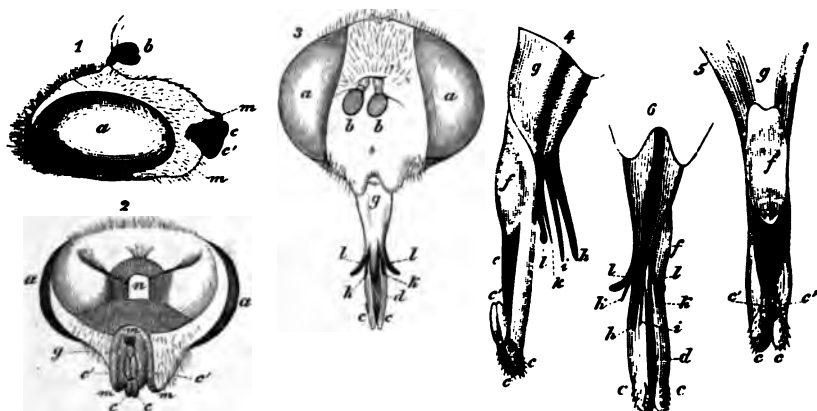


FIG. 4.—Mouth-parts of *Eristalis* (7:1).

1.—Head of *E. arbustorum* with retracted proboscis, from the side.

2.—Ditto, from below.

3.—Ditto, with extended proboscis, from above.

4.—Extended proboscis of *E. tenax*, from the side.

5.—Ditto, from below.

6.—Ditto, from above.

*a*, eye; *b b*, antennæ; *c c*, end-flaps of proboscis; *c' c'*, their inferior segment; *d*, groove on the upper side of the point of the proboscis; *e*, harder chitinous piece on the under side of the point of the proboscis; *f*, contractile middle part of the proboscis; *g*, contractile base of proboscis; *h*, upper lip (*labrum*), grooved underneath to receive the unpaired piece (*i*), which probably represents the two fused mandibles; *k k*, maxilla; *l l*, maxillary palps; *m m*, edges of the cavity on the under side of the head into which the whole proboscis is withdrawn; *n*, occipital foramen.

flaps or lips each of two parts (*c c* and *c' c'*), and on its upper surface a longitudinal groove. Of the chitinous pieces at the end of the first segment of the proboscis, only the superior unpaired one (*h*), which is prolonged under the membrane to the head, can be looked upon as an upper lip (*labrum*); the lower one (*i*) seems to be formed by coalescence of the two mandibles. The upper lip (*h*) forms, with its concave side, a groove directed downwards into which the piece *i* can be completely withdrawn; between the bases of these pieces *h* and *i*, when drawn wide apart, the small opening of the mouth can be seen. The free ends of the two chitinous

pieces *kk* arise on each side somewhat below the coalesced mandibles (*ii*), and bear palps on their outer sides; these are therefore, without doubt, to be looked upon as the maxillæ with their palps, while the basal parts of the maxillæ have coalesced with the base of the lower lip (*g*) (*labium*), and are dimly visible below the skin (4, *l'*, Fig. 4). The contractile piece (*f*) and the piece supported by the chitinous plate (*e*), form together the free superiorly-grooved anterior part of the lower lip; *f* and *e* probably represent the submentum and mentum. The flaps (*cc*) are probably not the palps but the modified paraglossæ borne on the ligula, though Burmeister prefers to consider them as labial palps.

Let us now consider how these structures are disposed, (1) when feeding on pollen; (2) when sucking honey; (3) when at rest.

(1). In feeding on pollen, the fly stretches out its extensible proboscis,<sup>1</sup> moving it, according to need, straight forwards, outwards, or upwards, grasps with the two flaps at its extremity a little mass of pollen, rubs this down to single grains by a rapid motion of the flaps, and passes it backwards by the same motion into the groove on the lower lip; in this groove lies the upper lip, which is grooved below, and, within that, the chitinous pieces which are presumably formed by coalescence of the mandibles, and are now prepared to seize the pollen. As soon as the pollen is sent backwards by the terminal flaps, these chitinous pieces separate slightly the parts which immediately surround the mouth-orifice, seize the pollen now lying in the groove of the lower lip, and thrust it backwards into the mouth. After a few seconds the first portion is swallowed, and the same series of actions begins anew. When the pollen-grains are united into long strings by elastic threads, as in *Ænothera*, an action of the forelegs, alternating with the movements just described, is necessary in order to free the pollen-grains from the threads. After the fly has torn away a little mass of pollen from the anther, it brings up its forefeet to its mouth while standing on its mid and hindlegs; then taking the cord of elastic threads between its forefeet, and rubbing them together as if washing its hands, it tears the threads asunder, and frees proboscis and legs from them. Sometimes, to clean the terminal flaps from adhering pollen, it takes its proboscis in its forefeet, and rubs it

<sup>1</sup> In *Eristalis tenax*, which attains a length of 15 mm., the outstretched proboscis is 7 to 8 mm. long; in *E. arbustorum*, which is 10 mm. long, the proboscis is 4 to 5 mm. long.

gently between them. A remarkable peculiarity of the flaps, shown in Fig. 5, makes them admirably adapted for seizing the pollen, for grinding it down, and for passing it backwards; the apposed surfaces of the two flaps being closely set with parallel ridges of chitin, by which the pollen-grains are easily held fast, and shoved into the entrance of the groove (*d*).

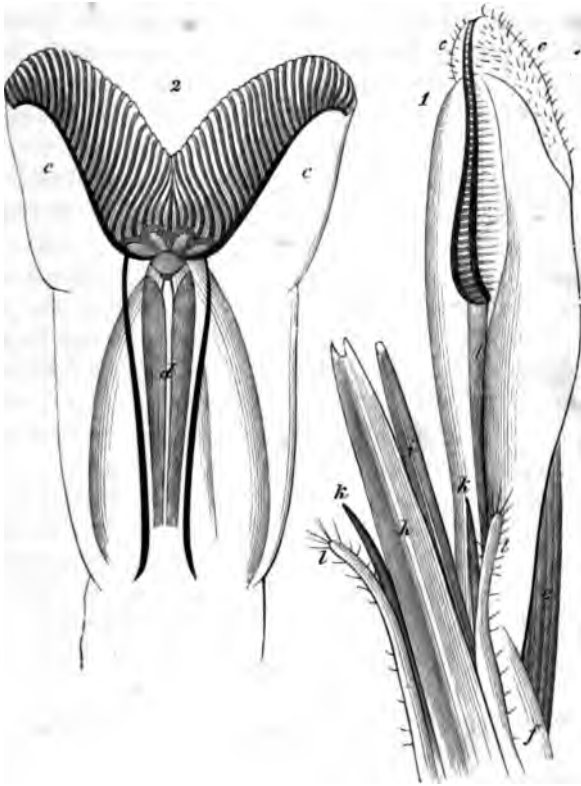


FIG. 5.—Proboscis of *Eristalis tenax*, more highly magnified.

1.—The greater part of the proboscis of *Eristalis tenax*, L., with the flaps applied together, and the mouth parts slightly separated; seen from above. When the pieces *h* and *i* are depressed in the groove *d*, the mouth parts are in the position for feeding on pollen.

2.—The end of the same proboscis with the flaps separated to show the chitinous ridges on their inner sides.

Lettering as in the preceding figure.

This peculiarity is undoubtedly developed in connection with a pollen diet, for it is obviously advantageous thereto; and it is only found in those families of Diptera which visit flowers to obtain both pollen and honey (*Syrphidæ*, *Muscidæ*, *Stratiomyidæ*), and is absent in those which avail themselves of honey only (*Bombyliidæ*,

*Empidæ*, and *Conopidæ*), and in the gnats, which are also purely suctorial.<sup>1</sup>

(2). In sucking honey the *Syrphidæ* place the grooved upper lip (*h*, 1, Fig. 5), and the chitinous piece (*i*) together, to form a tube which is inclined downwards and inclosed within the groove on the lower lip. The terminal flaps may now be useful in two ways; they may either be laid close together (as in 1, Fig. 5) while the membranous middle joint (*f*) of the lower lip is so far drawn in that the suctorial apparatus inclosed within the groove of the lower lip protrudes in front of the flaps and dips into the fluid to be sucked; or they spread out the flaps wide apart so that their rough inner surfaces rest upon the support, and the point of the suctorial apparatus protrudes at the end of the groove on the lower lip. Flies with swollen cushion-shaped flaps (*Syrphus balteatus*, Fig. 7) act usually in the latter way, those with long narrow flaps (*Rhingia*, Fig. 6) adopt exclusively the former. Both pollen-grains and fluid which have been carried into the tube formed by the chitinous pieces *h* and *i*, are aided in their passage to the mouth by means of the sucking stomach in connection with it. The maxillæ and their palps seem to play no part either in sucking or in feeding on pollen, and hence must be looked upon as useless appendages in the *Syrphidæ*.

(3). To guard the proboscis when at rest, the fly draws the membranous basal piece *g* backwards and downwards, the upper lip, mandible, and maxillæ, with their palps fold upwards, the contractile middle piece (*f*) is closely drawn up, forming a few membranous folds at the lowest part of the proboscis, the horny plate (*e*) and the flaps (*c*) fold upwards and forwards, and the whole proboscis now lies so deeply hidden in the deep cavity underneath the snout-like prolongation of the head (*m*, 1, 2, Fig. 4), that at most the terminal flaps protrude slightly (1, Fig. 4). On examining the head now from below (2, Fig. 4) one sees in the cavity only the flaps *c c'*, and beneath them the upper part of the chitinous plate (*e*), whose lower part lies hidden in the folds of the contractile part of the proboscis.

A further advance on these adaptations, fitting them still more completely for their threefold requirements, is conceivable, if to a still more elongated proboscis there is added a greater development of the snout-like prolongation of the head which covers it

<sup>1</sup> I have never observed the *Tabanidæ* to feed on pollen, though their end-flaps are roughened with chitinous ridges; but I have often found *Tabanus micans* and *T. luridus* on flowers, and I think it not unlikely that they sometimes feed on pollen.

when at rest. Such a state of things is found in *Rhingia*, where the proboscis (11 to 12 mm. long), exceeds in length the whole body (10 mm.), and is not surpassed by that of any indigenous fly.<sup>1</sup>

In anthophilous insects, the power to detect hidden honey advances parallel to the structural adaptations for securing it. When Sprengel described flies as stupid insects, incapable of finding out honey which lay concealed, that statement applied to the great majority of short-tongued forms, but not at all to forms with long proboscides, such as the *Syrphidæ*, *Bombyliidæ*, *Conopidæ*, and *Empidæ*.

*Rhingia* takes a foremost place in intellectual acuteness, as in the length of its proboscis, and there is, I think, no flower which affords honey attainable by it, that it does not discover and make use of. For instance, the deeply-hidden nectaries of the Iris are more frequently visited by *Rhingia rostrata*

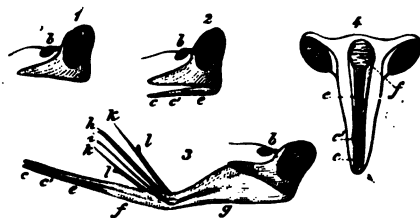


FIG. 6.—Proboscis of *Rhingia rostrata*, I.

- 1.—Side view of head with retracted proboscis.
- 2.—Ditto, at the moment when the proboscis begins to unfold.
- 3.—Ditto, with fully extended proboscis.
- 4.—Head, with retracted proboscis seen from below, twice as much magnified as in the three first figures.

Lettering as in Fig. 2.

than even by humble-bees, though Sprengel (p. 74) considers that no insects save bees can find them, and adds that this goes without saying in the case of flies, which are so obviously too stupid.

But even in the *Syrphidæ*, only a few species have acquired so highly specialised a proboscis as *Eristalis*: the great majority have a proboscis formed on a similar plan, shown in Fig. 7. The labium is much shorter, its extensible middle joint is wanting, the terminal flaps are swollen and cushion-shaped, and there is a corresponding diminution in intellectual power. Of the families of *Diptera* besides *Syrphidæ*, the *Muscidæ*, *Stratiomyidæ*, *Bombyliidæ*, *Conopidæ*, and *Empidæ* are of some importance in the fertilisation

<sup>1</sup> *Bombylius discolor*, Mik., alone equals it in the length of its proboscis; *Bombylius major*, L., approaches it (10 mm.)

forwards. The labrum itself is drawn out into a stiff, fine point. Both the labrum and the united mandibles, held between the long, narrow end-flaps (*paraglossæ*), may easily be stuck into soft tissues. I have often seen species of *Bombylius* thrust their tongues into honeyless flowers (e.g. *B. canescens*, Mik., into *Hypericum perforatum*), and I imagine that here the boring apparatus was being brought into action.

While, so far as I know, the species of *Bombylius* and the *Conopidæ* restrict themselves to the juices of flowers, very many other anthophilous flies are in the habit at times of sucking all kinds of other, often uncleanly, fluids. Thus, species of *Eristalis* may be seen feeding eagerly in gutters, *Scatophaga* and *Lucilia* on dung, *Sarcophaga* on putrid flesh; even *Volucella bombylans*, which is so abundant on flowers, I noticed in May, 1869, feeding on a floating carcase, and returning repeatedly to it when driven off. Several flowers seem to have acquired an offensive smell in relation to these habits of flies.

Of the second main division of Diptera, the gnats, the larger forms, *Tipula*, *Bibio*, etc., are of very second-rate importance in the fertilisation of flowers; they occasionally lick fully exposed honey, and so act now and then as carriers of pollen. No flower has become specially adapted for them. Tiny species of midges, on the other hand, e.g., *Psychoda phalaenoides*, which hide in dark corners in the daytime and fly actively in the evening, are the regular fertilisers of the remarkable flowers of *Aristolochia Clematidis* and *Arum maculatum*, which afford dark hiding-places for their visitors, and hold them in a temporary prison; others play an important part in the fertilisation of *Adoxa* and *Chrysosplenium*.

The group of Thysanoptera (*Thrips*) are by their small size (hardly 1 mm. long at most, and many times less in breadth) fitted far better than even the *Anthocoridæ* among the Hemiptera or *Meligethes* among the beetles, for entering all sorts of flowers. Probably few flowers, if any, are altogether exempt from their visits, and though they have seldom been detected in the conveyance of pollen, yet from their great abundance their value as fertilisers must not be overlooked. It must be almost impossible to exclude these tiny insects, when we try to isolate a plant experimentally by means of nets.<sup>1</sup> The Thysanoptera seek both pollen and honey. They seize a single pollen-grain in their

<sup>1</sup> Darwin, whose experiments were always marked by admirable precautions, always kept in view the possibility of Thysanoptera entering through his nets.

mandibles, and convey it to the mouth; they obtain honey by applying the mandibles and maxillæ together so as to form a short, conical sucking-apparatus. Besides a floral diet, they avail themselves, according to Westwood, of other plant-juices;<sup>1</sup> they injure,

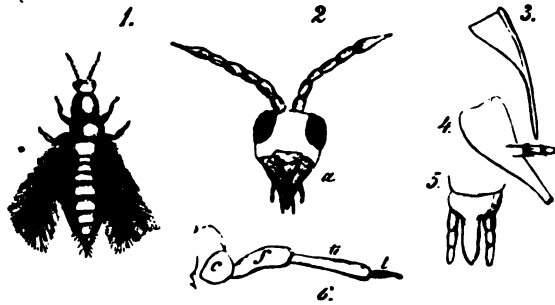


FIG. 9.—*Thrips* (Black-fly).

- 1.—*Thrips*, seen from above ( $\times 30$ ).  
 2.—Its head, more highly magnified, front view.  
 3.—Mandible. 4.—Maxilla. 5.—Labium.  
 6.—Leg. *c*, coxa; *f*, femur; *t*, tibia; *t*, tarsus, on the end of which is a sucking disc instead of hooks.

for example, cucumbers and melons, and leave the leaves on which they have settled dotted over with small dead spots. Thus they agree with *Diptera* in availing themselves both of pollen and honey, and in not restricting themselves to a floral diet.

We may here mention the young larvæ of *Meloë*, called by Kirby<sup>2</sup> *Pedicularis Melittæ*, and by Dufour *Triungulinus*, which resemble the *Thysanoptera* in the activity of their movements, and in their minute size which permits entry into all flowers. Although they visit flowers only to attach themselves as parasites to bees, they feed for the time on pollen and honey, and getting thus dusted with pollen they play a part similar to, but even more subordinate than, that of the *Thysanoptera*.

### Hymenoptera.

The order of *Hymenoptera* takes a still higher rank than the *Diptera* in regard to its adaptations for a floral diet and its importance in fertilisation; for the great majority of its members, in the perfect state, are entirely dependent upon flowers. Reviewing the main divisions of this order, the Wood-borers (*Sirex*, L.) are the only forms which I have never found upon flowers; of the ants several species, of the Saw-flies (*Tenthredo*), Ichneumons (*Ichneumon*,

<sup>1</sup> *Introduction to the Modern Classification of Insects*, ii. p. 4.

<sup>2</sup> *Monographia Apum Angliæ*, pl. xiv. fig. 10.

*Bracon*), Chalcididæ (*Pteromalus*), and Ruby-tails (*Chrysis*), many species, of the Wasps (*Diploptera*) and Sand-wasps (*Fossores*), almost all which I have had the opportunity of observing, and of the bees all species without exception, rely almost exclusively on a floral diet.<sup>1</sup>

All these groups, excepting the last two, are only capable of sucking honey from flat exposed surfaces, and even among the Sand-wasps there are few species whose proboscis can reach some millimetres into a tubular flower; so that a large proportion of flowers are exempt from the visits of all Hymenoptera except bees. But bees, which not only feed when in the perfect state exclusively on the produce of flowers, but nourish their young thereon also, are in such intimate and lifelong relations with flowers, that they show more adaptations for a floral diet, and are more important for the fertilisation of our flowers, and have therefore led to more adaptive modifications in these flowers, than all the foregoing orders put together. A closer study of bees is therefore essential for a right understanding of the fertilisation of many of our flowers.

### The Family of Bees.

The various structural modifications in bees will be most easily understood, if we arrange them in the natural order of genetic descent. For the grounds of my views, I must refer the reader to a special essay of mine on the subject of bees.<sup>2</sup> If my conclusions are correct, bees are descended from certain Sand-wasps, which, like the species at present existing, pursued spiders, insects and their larvæ, disabled them with their sting, carried them to their nests, and laid an egg beside each, thus supplying the resulting larva with living food,—while the perfect insects fed entirely on honey and pollen; these were the founders of the new race, who gave up the old manner of feeding the young to feed them with a portion of their own food, disgorged from their stomachs. The race thus started differed at first from the others in nothing but this habit; but in the course of time, filling an unoccupied place in the economy of nature, they increased

<sup>1</sup> For a discussion of the genealogical relations of the families of Hymenoptera and their gradual acquirement of proficiency in anthophilous habits, consult my recent works, "*Wie hat der Honigbiene ihre geistige Befähigung erlangt?*" (*Eichstädter Bienenzeitung*, 1875, 1876; and note in *Nature*, vol. xv. p. 178) and "*Die Entwicklung der Blumenthätigkeit der Insekten*," ii. and iii.

<sup>2</sup> "*Anwendung der Darwin'schen Lehre auf Bienen*," *Verh. der naturh. Ver. für pr. Rheinl. u. Westfal.* 1872, pp. 1-96.

enormously, and at last formed the widely ramified family of bees; the still extending branches of this family, our recent bees, show us in many ways gradations in their adaptations to a floral diet, which help us to recognise to some extent the lines of their evolution.

The species of *Prosopis* stand just on the same level with the primitive ancestral types of bees. In their almost hairless bodies, the narrow first tarsal joint, scantily provided with hairs (Fig. 10, *t'*), and their very slightly elongated mouth-parts, they completely resemble the Sand-wasps, and only claim to be admitted to the family of bees by their manner of feeding the young. They fill

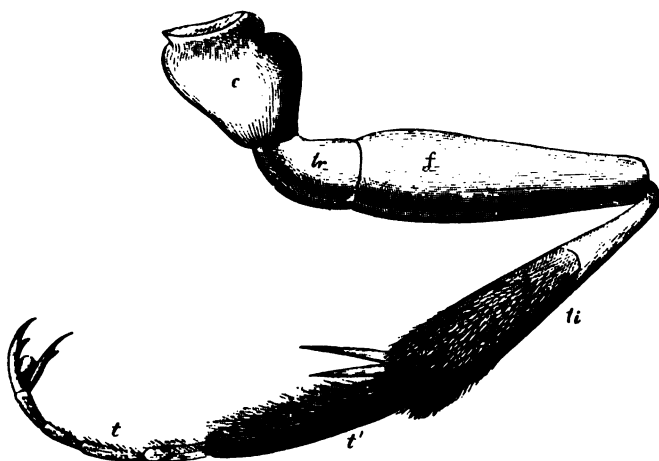


FIG. 10.—Right hindleg of *Prosopis variegata*, ♀. Seen from behind.  
c, coxa; tr, trochanter; f, femur; ti, tibia; t, tarsus; *t'*, first joint of tarsus.  
(The tibia and tarsus are drawn too hairy).

their brood-chambers (which are lined with a hard cement by means of the broad tongue) with a mixture of disgorged honey and pollen, which serves as food for the larvæ on hatching. These little active insects, which themselves have a peculiar odour, prefer strongly scented flowers, *Reseda*, *Ruta*, *Lepidium sativum*, *Matricaria*, *Achillæa*, etc., where they alternately suck honey and eat pollen. In spite of their smooth bodies, sticky pollen adheres frequently to them, especially to the parts of the mouth and to the slightly hairy legs; these have feebly developed brushes on their tarsi (Fig. 10, *t'*), by which the bee can clean the whole upper surface of its body after burrowing, but no other part of the body has any development of hairs suited for collecting pollen.

Though the species of *Prosopis* are thus no better fitted for a floral diet than many Sand-wasps, they are of far greater importance as fertilisers on account of their more frequent visits to flowers, in procuring food for the young. We must consider minutely the form and action of their mouth-organs, to understand the higher

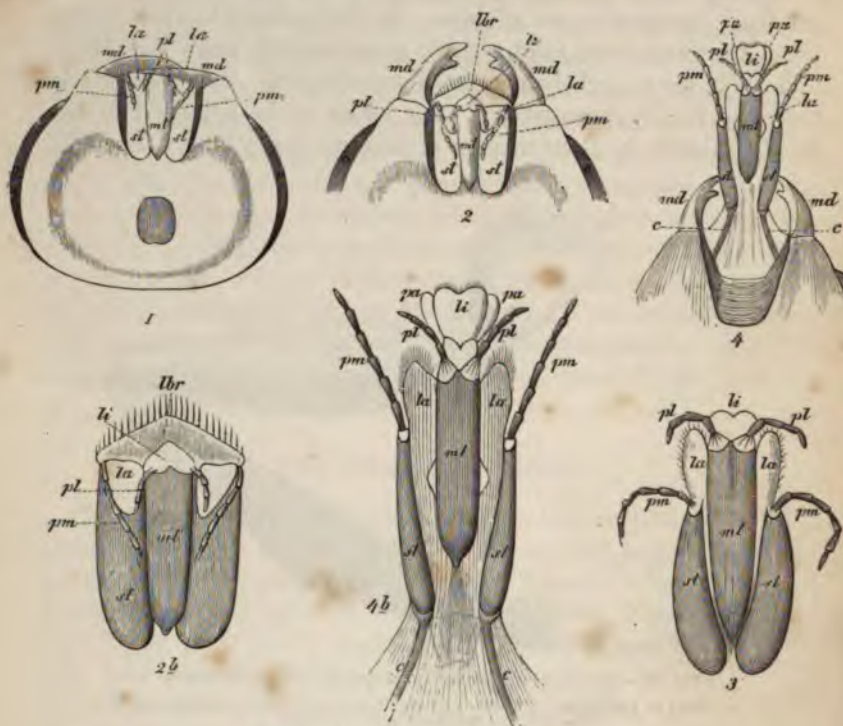


FIG. 11.—Mouth-parts of *Prosopis*.

- 1.—Head with completely folded mouth-parts. Seen from below.
  - 2.—Front part of head, after the mandibles have diverged and the labrum turned upwards.
  - 2b.—Mouth-parts in the same position; more highly magnified.
  - 3.—Mouth-parts, after elevation of the maxillae, maxillary and labial palps, and with the tongue partly extended; magnified as in 2b.
  - 4.—Ventral view of front region of head after complete extension of the mouth-parts; magnified as in 1 and 2.
  - 4b.—The completely extended mouth-parts; magnified as in 2b and 3.
- lb, labrum; ma, mandibles; c, cardo; st, stipes; la, lamina; pm, maxillary palp; mt, mentum; li, ligula (tongue); pa, paraglossae; pl, labial palp; o, eye.

and more specialised forms of mouth in bees. When at rest (1, Fig. 11), the maxillae and labium in *Prosopis* are withdrawn into a cavity on the lower surface of the head, which they completely fill. They are retracted, not as in flies, by the contraction of a membranous piece into transverse folds, but by the folding up of stiff chitinous pieces jointed together. The two basal pieces or

*cardines* of the maxillæ (*cc*, 4, Fig. 11), are hinged by two joints to the sides of the cavity below the head, so that they can rotate backwards and forwards. In the state of rest they are bent backwards; the next segments (*stipites*) (*st*), and the mentum which is placed between, are drawn back, so as to cover the *cardines* completely. The laminæ of the maxillæ (*la*), with their palps (*pm*) and the labial palps (*pl*), are also folded over, downwards and backwards, and the mandibles (*md*) are laid over the bases of these parts, and also cover the retracted tongue (*li*) and the downward-folded upper lip (*lbr*, 2, Fig. 11). In the state of rest, the mandibles alone are free to act, without any other part of the mouth changing its place. When they are separated (2, Fig. 11), the upper lip, the tongue, the bases of the retracted maxillæ, the maxillary and labial palps, come into view.

When the bee wants to suck honey, it extends its maxillæ and maxillary and labial palps forwards, and spreads out its tongue (3, Fig. 11); then turning the *cardines* of the maxillæ forward (*cc*, 4, Fig. 11) on their hinges, the maxillæ and labium (mentum and tongue) are advanced by twice the length of these *cardines*, and the tongue may now be introduced into honey-receptacles if not too deep or narrow.

The Sand-wasps possess in quite a similar manner the power of folding up the lower parts of the mouth to bite, and extending them to suck, and so *Prosopis* can show no advance in fitness for a floral diet beyond the ancestors of the bees. The only peculiarity which *Prosopis* has developed is the habit of lining its brood-cavities with slime, which hardens into a thin shell; this habit necessitates a short, broad tongue, and therefore prevents the development of a long tongue fitted for obtaining deeply-seated honey.

Considerably higher in the scale than *Prosopis*, in regard to such adaptations, are *Sphecodes*, and the closely allied, but still more specialised genera, *Halictus* and *Andrena*. In all three, the tongue (*li*, 4, Fig. 12; 1, Fig. 13) is moderately short, and is enabled to reach more deeply-placed honey, not so much by its own length as by the increased length of the mentum and the *cardines*. Unlike *Prosopis*, the tongue here is pointed, and more or less covered with hairs and fine transverse lines at the tip; since it has become more freed from the task of nest-building,<sup>1</sup> it has grown narrower and more elongated in many species of *Andrena* and *Halictus*, to

<sup>1</sup> These genera line their brood-cavities, which are generally subterranean, with very little slime.

be of greater service in honey-getting (1, Fig. 13). In a state of rest, the lower parts of the mouth are even more securely hidden, and the mandibles can move even more freely, in *Sphecodes* and many species of *Halictus* than in *Prosopis*, for the upper lip (*lbr*, 2, Fig. 12) folds down and completely covers the laminae and maxillary and labial palps.

The three genera *Sphecodes*, *Halictus*, and *Andrena* have advanced farther from the state of the ancestral bees in regard to the development of their hairy coat than of their mouth-parts. *Sphecodes* has made the first step in advance; *Halictus* and *Andrena* have proceeded farther.

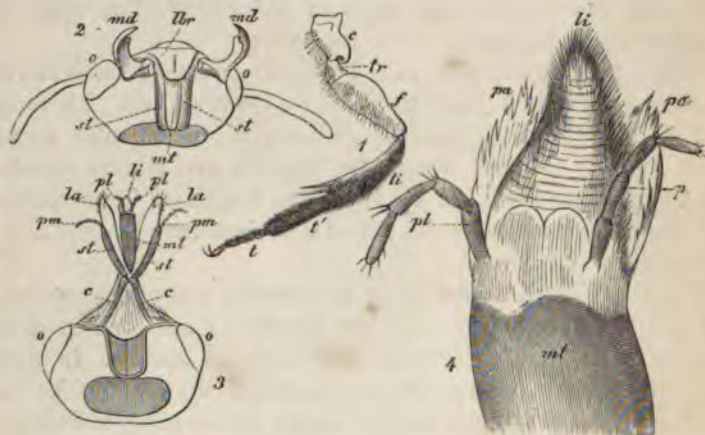


FIG. 12.—*Sphecodes*.

1.—Right hindleg of *S. gibbus*, L. ♀., hind view. Lettering as in Fig. 10.

2.—Head, with mandibles opened, but the lower mouth-parts folded and hidden by the labrum.

3.—Head, after removal of the mandibles and labrum, with unfolded and protruded mouth-parts.

4.—End of labium, more highly magnified.

Lettering of 2, 3, 4, as in Fig. 11.

In *Sphecodes* the whole body is sparingly covered with hairs which show the first traces of feathery branching; the legs are more thickly clothed with hairs, especially the outer side of the tibiae of the hindlegs (*ti*, 1, Fig. 12); the tarsi (*t'*, 1, Fig. 12) are about as narrow as in *Prosopis*, but the brushes on their inner side are a little better developed. The species of *Sphecodes* feed their young in a most primitive manner, viz. on the disgorged surplus of their own food; yet they certainly derive advantage from the hairy covering on their body and hindlegs, for the pollen which sticks there in their visits to flowers they wipe off with their tarsal brushes and use incidentally as food for themselves or their young.

In the exceedingly numerous species of *Halictus* and *Andrena*, the hairy covering of the hindlegs has so increased, and the development of tarsal brushes has become so perfect, that the practice of feeding the young on pollen collected by these hairs, which was only a secondary matter in *Sphex*, is here exclusively or mainly relied upon.<sup>1</sup> The collecting hairs are spread over the whole hindleg from the tibia to the coxa (2, Fig. 13); even the last joint of the thorax sometimes bears two large tufts of hairs,

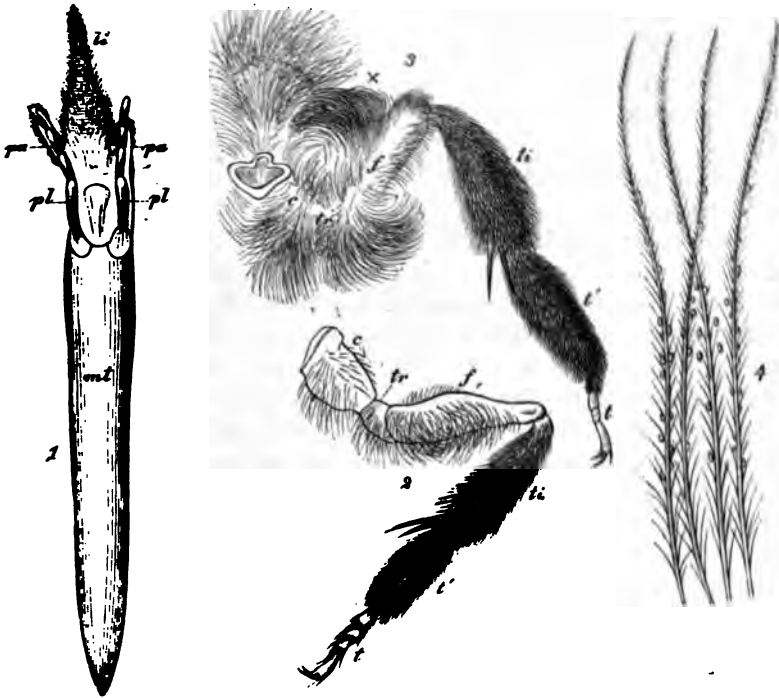


FIG. 13.—*Halictus* and *Andrena*.

- 1.—Labium of *Halictus quadricinctus*, F. ♀. *ml*, mentum; *li*, ligula (tongue); *pa*, paraglossae; *pl*, labial palp.
- 2.—Right hindleg of the same bee.
- 3.—Metathorax and right hindleg of *Andrena pratensis*, Nyl. ♀; *x* right tuft of hair on metathorax. Lettering in 2 and 3 as in Fig. 10.
- 4.—Single hairs from the body of an *A. pratensis* taken on a willow. Numerous pollen-grains adhere to their feathery branches.

under which considerable masses of pollen can be lodged (3, Fig. 13). By a notable increase in breadth of the tarsi, the carrying-power of the tarsal brushes is increased.

<sup>1</sup> I have occasionally observed species of *Andrena* and *Halictus* feeding on pollen, and I have seen captive specimens disgorge drops of honey yellow with pollen grains

In *Andrena* and *Halictus*, although the chief supplies of pollen are obtained by means of the hindlegs, yet in these and in all other hairy bees the hairy covering of the body is undoubtedly of advantage. In many flowers this gets dusted without any direct effort with a considerable quantity of pollen, which is then cleared off by means of the tarsal brushes. In almost all bees highly specialised for a floral diet, we find the body more or less thickly clothed with long feathery hairs.

The development of the hairy covering is of the highest importance for the fertilisation of flowers. For as the hairs easily take up pollen, they give it up again as easily to viscid or rough stigmas. It would far exceed the limits of our space to discuss the adaptive modifications present in all the groups of our indigenous bees. I can only explain the further development of the pollen-collecting apparatus and of the lower parts of the mouth by a few examples.

We have seen in *Sphecodes*, *Halictus*, and *Andrena*, how the development of pollen-collecting hairs has gradually reached an extreme pitch on those parts of the body where the burden is least endangered by the movements of flying and creeping; viz. on the whole of the hindleg from the tarsus to the coxa, and on the hind part of the thorax. In forms higher than *Andrena* and *Halictus*, this collecting apparatus has attained still greater perfection, in getting more and more restricted to those sections of the hindleg to which the tarsal brushes can most readily apply the pollen that they have collected, viz. the tarsus and tibia. In the highest forms, this localisation of the collecting-hairs has been attained without diminishing the mass of pollen, by an increased growth of hairs on the tibia and tarsus and a withdrawal of the more distal hairs: this we see most clearly in *Dasypoda* and *Panurgus*.

In *Dasypoda* (1, Fig. 14), the collecting-hairs of the tibia and tarsus have become so long that they can carry a much greater load of pollen than the far more extensive collecting apparatus of *Andrena pratensis*, Nyl. (3, Fig. 13); but the hairs on the femur, trochanter, and coxa, are long and thick enough to take a large share in the work. In *Panurgus* (2, Fig. 14), the collecting apparatus consists solely of the long hairs upon the tibia and tarsus. A further advance is seen in *Eucera* and *Anthophora*, where an increase in breadth of the pollen-collecting surfaces of the tibia and tarsus compensates for the shortening of the collecting-hairs.

The last step in the evolution of the collecting apparatus on the

hindlegs was attained through a new habit, which rendered possible a great economy of collecting-hairs, and a great saving of time in emptying the collecting apparatus and preparing the larval food. This was the practice of moistening the pollen with honey before placing it in the collecting apparatus, so as to form one connected mass which could be easily removed from the collecting apparatus, and at once used to feed the larvæ.

*Macropis* (1, Fig. 15) is in this way able to carry large balls of pollen mixed with honey on its hindlegs, though the tarsus and tibia are clothed with comparatively short hairs (2, Fig. 15).

In *Bombus* (3, Fig. 15) we have a still farther advance. The pollen is kept entirely to the outer side of the hindlegs, which



FIG. 14.—Localisation of collecting-hairs on the tibia and tarsus.

- 1.—Right hindleg of *Dasypoda hirtipes*, F. ♀, seen from behind and within ( $\times 7$ ).
- 2.—The same leg of *Panurgus Bankianus*, K. ♀ ( $\times 7$ ).
- 3.—The same leg of *Anthophora (Saropoda) bimaculata*, Fz. ♀ ( $\times 7$ ).

Lettering as in Fig. 10.

leads to a still greater economy in collecting-hairs. For the outer surface of the tibia of each hindleg is perfectly smooth, and only surrounded at the edge with a fence of long hairs, some erect, some bent inwards, forming a kind of basket, in which the pollen-mass can be heaped high over the brim. So that not only is there a saving of collecting-hairs, and a saving of time in unloading the collecting apparatus, but the tarsal brushes of the hindlegs, which even in *Macropis* got charged with pollen, here resume their free use as brushes.

*Apis*, finally, stands on a higher level than *Bombus* in the arrangement both of its collecting apparatus and its tarsal brushes.

While in *Bombus* the collecting basket is walled in by many irregular rows of stiff hairs, still showing traces of the feathery branching of the primitively undifferentiated hairy coat, in *Apis* (5, 6, Fig. 15) these hairs have become simple smooth bristles with no trace of feathery branching, and arranged in a few close-set rows. The bristles of the tarsal brushes in *Apis* (t' 5, Fig. 15) are arranged in regular rows, and much more uniformly than in *Bombus* (t' 3, Fig. 15); and the now functionless tibial spurs, inherited from the Sand-wasps, which, with most other bees, they aid in making holes in earth, rotten wood, etc., have disappeared from the hindlegs.

The collecting apparatus of the hindlegs, which culminates in the hive-bee, is peculiar to one of the two main divisions of bees;



FIG. 15.—Last grades of perfection of the pollen-collecting apparatus of the hindleg.

- 1.—Right hindleg of *Macropis labiata*, Fz. ♀. Seen from behind and within.
- 2.—The same laden with pollen of *Lytmachia vulgaris*.
- 3.—Right hindleg of *Bombus Scrimshirianus*, K. ♀. Seen from behind and within.
- 4.—Its tibia, seen from the outside (pollen-basket).
- 5.—Right hindleg of honey-bee (*Apis mellifica*, L. ♀). Seen from behind and within.
- 6.—Its tibia, seen from the outside.

Lettering as in Fig. 10.

No. 1 naturally shows only a side view of the hairs on the outer surface of the tibia and tarsus of *Macropis*.

in the other division a collecting apparatus is formed by hairs on the ventral surface of the abdomen. In these forms, at least in our native species, we cannot trace a gradual development of the collecting apparatus as in the others; but it possesses the same main features in all genera of the group (*Heriades*, *Chelostoma*, *Anthidium*, *Osmia*, *Chalicodoma*, *Diphysis*, *Megachile*); so that one example will suffice for all.

The whole or nearly the whole ventral surface of the abdomen is covered with a brush of stiff bristles inclined backwards, which

vary in length, closeness, and colour in different species, but are always smooth, without trace of feathery branching. This abdominal collecting apparatus differs also in its action from the collecting apparatus on the legs of the other forms; in the latter, the tarsal brushes (formed of smooth stiff bristles) sweep the pollen into the tufts of feathery hairs; in the present case, the collecting apparatus consists of a great brush of feathery hairs, which themselves sweep up the pollen. More than nine-tenths of the flowers visited by bees with abdominal brushes are such as are adapted to dust the ventral surface of the bee with pollen (*Echium*, *Papilionaceæ*, *Compositæ*, etc.) without any action of the tarsal brushes. Bees with abdominal brushes may be seen, for instance, upon a composite flower, thrusting their tongues quickly into one floret after another, and at the same time turning round bodily so as to force the pollen which lies free on the surface of

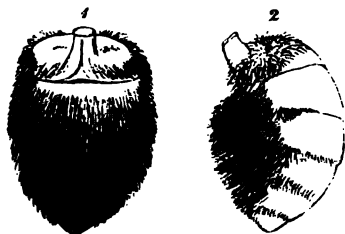


FIG. 16.—Abdominal collecting apparatus.

- 1.—Abdomen of *Osmia spinulosa*, K. Ventral view. ( $\times 7$ )  
2.—Lateral view of the same. ( $\times 7$ )

the capitulum between the hairs of the brush. The brush is quite full after visits to a few capitula. I have, for instance, very often seen *Megachile lagopoda*, K., acting in this manner on *Onopordum acanthium*, and *Osmia spinulosa*, K., on *Carduus acanthoides*. More rarely, bees with abdominal brushes may be seen feeding on flowers whose pollen gets applied to their backs; in such cases, the bee makes use of its tarsal brushes to sweep off the pollen from the parts where it has fallen into the abdominal brushes. I have seen *Anthidium manicatum* acting in this manner on flowers of *Ballota nigra*.

The latter mode of getting pollen is adopted only exceptionally by bees with abdominal brushes; the plan of sweeping it up directly is their usual method, and is quicker and more productive than the method used by bees whose collecting apparatus is on their legs. There can be little doubt, therefore that the bees with

abdominal brushes have adapted themselves to the flowers which were fitted to dust their ventral surfaces (*Papilionaceæ*, *Compositæ*, *Echium*, etc.), and the contrary view, that these flowers have become adapted to the bees, is untenable, for the flowers are visited and fertilised by other and far more numerous insects; still more untenable is Delpino's idea (e.g. in regard to *Heriades truncorum* and *Helianthus*) of mutual predestination.

While a pollen-collecting apparatus, as we have seen, has been developed in very different ways in the two main divisions of the family, the adaptation of the mouth-parts for deeply-placed honey has advanced similarly in both. In both, a natural limit to the length of the cardines and of the mentum (by which, in *Prosopis*, *Sphecodes*, *Halictus*, and *Andrena*, increased protrusibility of the tongue was attained) has been fixed by the length of the head, underneath which these parts must be withdrawn to give play to the mandibles; and access to more deeply-placed honey is got by lengthening the tongue itself, and by extension of the membranous and elastic parts between the mentum and the cardines.

In the higher forms of both groups, we find that the tongue, which was at first much shorter than the mentum, and retractile into it, is many times as long as the mentum; the transverse markings (absent in *Prosopis*, slight in *Sphecodes*, well-marked in *Halictus*) are present as strongly-marked transverse rings over the greater part of the vermiform tongue; the hairs of the tongue, which have scarcely a definite arrangement in the lower forms, form whorls upon each transverse ring, and can be erected or depressed forwards, and the originally membranous and elastic parts between the mentum and cardines are elongated and supported by chitinous pieces, in such a way that when these fold together the mentum is retracted between the stipites as far as the ends of the cardines, and can be again protracted for the full length of the chitinous pieces.

With these modifications of the lower lip, certain changes in the maxillæ are closely associated, and advance similarly in both divisions of the family. As soon as the tongue has so far increased in length that it can no longer be quite withdrawn into the anterior hollow of the mentum, it comes to be folded up downwards and backwards, and both in the retracted and in the extended state it is concealed between the laminæ to avoid injury in nest-building or in being introduced into honey-receptacles. The laminæ, once devoted to the service of the tongue, elongate *pari passu* with the tongue itself; and correspondingly the labial palps and at first also

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the maxillary palps elongate also, in order to act still as organs of touch. But the maxillary palps are soon outstripped by the laminæ, the labial palps, and the tongue, and becoming useless gradually abort; the laminæ and labial palps continue to advance to the full extent of elongation of the tongue. This difference is explained by the rise of a new function which the labial palps and laminæ assume, and which renders them quite indispensable and renders the maxillary palps quite unnecessary. For as the tongue elongates, the laminæ develop more and more into a sheath closely surrounding the tongue, which not only protects it in retraction and when being thrust into a tubular flower, but also comes to

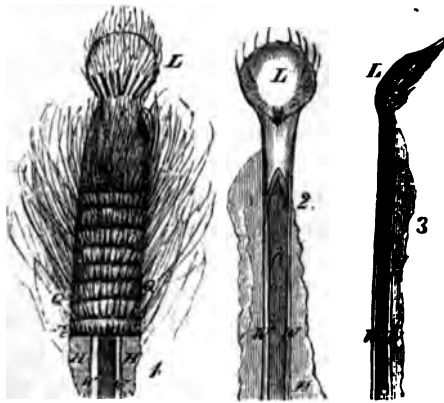


FIG. 17.—Tip of Hive-bee's tongue. Highly magnified.

- 1.—End of tongue, seen from above. The covering bearing the whorls of hairs (Q) is torn away at G to expose the capillary tube.
  - 2.—The capillary tube with the covering removed, and opening into the spoon-shaped hollow. Seen from below
  - 3.—Side view of the same.
- C, capillary tube; W, its wall; H, skin adhering to the capillary tube; G, ring, formed by the expanded bases of the hairs; Q, whorls of hairs; L, spoon-shaped hollow.  
In 1 the hairy, concave upper side is seen; in 2 the lower, convex, nearly naked side.

play the **part** of a suction-tube, in which the tongue, perhaps by a progressive erection from before backwards of the whorls of hairs, conveys the honey taken up at its point back towards the mouth. In this the labial palps are also concerned, for their two or three proximal joints become flattened and help the laminæ in closely surrounding the tongue, while the last joint or the two last retain their original function as organs of touch. As soon as the proximal joints of the labial palps have come in this manner to form **part** of the suctorial apparatus, they naturally elongate *pari passu* with the tongue and the laminæ, and get transformed into long, thin,

chitinous plates surrounding the tongue, while their terminal parts, still acting as tactile organs, retain their original form, their shortness, and their free position. The maxillary palps, originally six-jointed, get handed down as useless heirlooms, and show all stages of abortion from six joints to none.

A final increase in the length of the tongue over that of the organs which insheathe it is got by making the proximal part of the tongue coil twice round and be retracted into the hollow end of the mentum; so that the tongue, which in the retracted state reaches quite to the end of its sheath, may be protruded by about the whole length of the sheath beyond it. As subordinate adaptations in the suctorial mechanism of bees, we have sharpening of the ends of the laminæ to pierce succulent tissues, and the development of a membranous lobe at the end of the tongue. In the less specialised bees, the tongue is supported throughout its whole length by a chitinous ridge; this in the higher forms becomes a capillary tube which opens out into the spoon-shaped hollow of the terminal lobe. As soon as the terminal lobe reaches the honey, a little honey ascends the capillary tube to the taste-organs, and the bee may judge at once whether to continue sucking or not.<sup>1</sup>

To follow out in detail the increasing complexity of the mouth in bees, through all its stages, would be a work of special entomological interest, as profitable as it would be comprehensive. Having studied the first adaptations to a floral diet in *Sphecodes*, *Andrena* and *Halictus*, we must pass over the manifold intermediate forms,<sup>2</sup> and investigate the complex mechanism of the mouth in the most specialised bees. I select for illustration the mouth of those bees which of all insects play by far the most important part in fertilising our indigenous flowers; viz. humble-bees (*Bombus*) and the hive-bee (*Apis*).

When we see the mouth-parts of these bees fully extended and artificially separated (Fig. 18, 1 and 2), it seems at first sight hardly possible that a suctorial apparatus so large and complex, which many times exceeds the head in length, can be as completely received into a cavity below the head as it is in the least specialised bees; yet this takes place by help of the four folding

<sup>1</sup> Wolff, *Das Riechorgan der Biene*, 1874; Hermann Müller, *Wechselbeziehungen*, p. 30. In the German edition of this book, 1873, the lobe is said to be employed probably in licking flat surfaces of honey.

<sup>2</sup> Some of these intermediate forms are figured in my essay, "Anwendung der Darwin'schen Lehre auf Bienen" (*Verhandl. des naturhist. Vereins für pr. Rheinland und Westfalen*, 1872).

movements already mentioned, whose various actions we must now consider.

(1.) When the bee is sucking honey which is only just within its reach, all the movable joints of its suction-apparatus, cardines, the chitinous retractors at the base of the mentum, laminæ, labial palps, and tongue, are fully extended, as in Fig. 18, except that the two proximal joints of the labial palps are closely applied

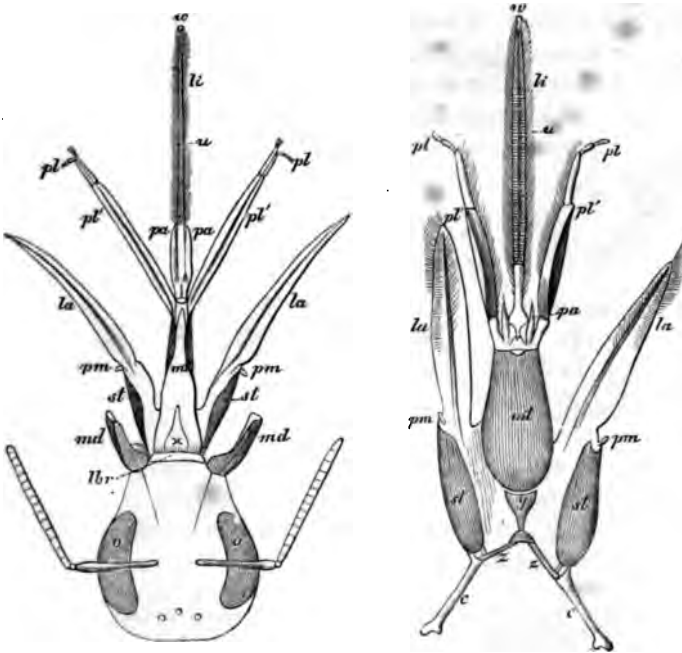


FIG. 18.

1.—Head of *Bombus agrorum*, F. ♀, with completely extended and separated mouth-parts. Seen from above ( $\times 5$ ).

2.—Mouth-parts of the Hive-bee, in the same position. Seen from below ( $\times 12$ ).

*pl'*, the lower joints of the labial palps modified as a tongue-sheath; *x*, piece covering the mouth, which lies between *x* and *ml* (*epipharynx*, Westwood); *y*, submentum (*fulcrum*, Kirby); *ss*, retractors, *i.e.* those chitinous pieces which unite the submentum with the ends of the cardines, and as they revolve backwards round the ends of the cardines, retract the mentum and its appendages. (Kirby calls *ss* the cardines, and *cc* lora.)

to the tongue below, and the laminæ to the mentum and hinder part of the tongue above. But as soon as the whorls of hairs at the point of the tongue are wet with honey, the bee by rotating the retractors (*zz*, Fig. 19) draws back the mentum, and with it the tongue, so far that the laminæ now reach as far forward as the labial palps (*i.e.* to the point *u* in Fig. 18); and now laminæ and labial palps together, lying close upon the tongue and overlapping

at their edges, form a tube out of which only the part *uw* of the tongue protrudes. But almost simultaneously with these movements, the bee draws back the basal part of its tongue into the hollow end of the mentum, and so draws the tip of the tongue, moist with honey, into the tube, where the honey is sucked in by an enlargement of the foregut, known as the sucking stomach,<sup>1</sup> whose action is signified externally by a swelling of the abdomen.<sup>2</sup>

Fig. 19 represents the head of a humble-bee in the suctorial position. If now the base of the tongue is drawn back into the hollow of the mentum (as shown in Fig. 20), the tip (*uw*) is drawn, wet with honey, into the tube. If the cardines (*c*, Fig. 19),



FIG. 19.—Head of *Bombus hortorum*, ♀, with proboscis half extended.

Seen from the side ( $\times 7$ ). Lettering as in Figs. 11 and 18.

which are now directed vertically downwards, are rotated backwards, the base of the suctorial tube (at *pm* in Fig. 19) will be drawn back to the opening of the mouth (between the base of the mandibles and upper lip), and by a sucking action of the sides of the body [and (?) a simultaneous action of the erectile hairs on the tongue<sup>3</sup>], the honey is quickly carried into the mouth.

<sup>1</sup> In *Apidae* and *Vespidæ* the "sucking stomach" is simply a lateral fold of the foregut; in *Crabronidæ* it is a vesicle attached by a short, narrow duct, much as in *Diptera*.

<sup>2</sup> Cf. the remarks on *Lamium album*.

<sup>3</sup> I came to the above conclusion with regard to the action of the whorled hairs from experiments made on bees and humble-bees under chloroform. In these, sometimes, if the tip of the tongue was dipped in syrup before complete loss of consciousness, the suctorial movements took place so slowly that their separate stages could be

By now rotating the cardines (*c*) forwards, the whole suction-apparatus is carried forward by twice the length of the cardines. The retractors (*z z*) are now rotated forwards in their turn, and a further advance of twice their length is given to the mentum (*mt*) with its appendages, to the labial palps, and to the tongue, while the maxillæ remain in their place, and their laminæ now inclose only the mentum and the hinder part of the tongue. Finally, the basal part of the tongue contained within the hollow part of the mentum is projected forth, and the tip of the tongue now reaches its farthest extension (20 to 21 mm. from the mouth in *Bombus hortorum*), and dips again into the honey at the base of the flower.

In flowers which contain abundant honey, a humble-bee may be seen to perform the act of sucking four or five, or sometimes even eight or ten times, the tip of the tongue being each time dipped into the honey, then drawn back into the sheath, and the sheath brought up to the mouth.

(2.) To reach honey which lies less deeply, the bee need not rotate the retractors (*z*); the tongue therefore remains constantly insheathed by the laminæ and labial palps, and only the basis of the tongue moves in and out of its cavity in the mentum, bringing its tip in and out of the extremity of the suctorial tube.

(3.) When the bee flies from one flower to another, it carries the proboscis<sup>1</sup> extended, so as to introduce it in the act of alighting into the tube of the flower; but the tongue is concealed within its sheath, to protect the delicate whorls of hairs, and to let the terminal joints of the labial palps perform their function of tactile organs.

So in flying from flower to flower the base of the tongue is contained within the hollow of the mentum, and the retractors (*z*) are directed backwards, while the cardines may be directed downwards (Fig. 19), forwards (Fig. 18, 2), or backwards, according to the depth of the flower which the bee has in view.

clearly distinguished; they were as described above. What went on between the chitinous plates of the laminæ and labial palps was of course invisible, but when these parts were drawn aside, a progressive erection of the whorls from the tip of the tongue backwards, could sometimes be clearly seen. The fact that the basal part of the tongue, which gets drawn into the hollow of the mentum, is free from whorls, seemed to stand in accordance with this action. At the same time, special muscles for the erection of the whorls are not present; and therefore my explanation becomes unsatisfactory. In several Brazilian bees, my brother Fritz Müller has found that the hairs of the tongue are transformed into stalked scales, which seem hardly fitted to drive the honey mouthwards by erection. In an undescribed azure-blue *Euglossa*, the imbricated scales seem to form a tube round the tip of the tongue, so that here suction may perhaps go on, without the tip of the tongue being withdrawn into the sheath formed by the laminæ and labial palps.

<sup>1</sup> The whole suctorial apparatus is thus designated for shortness' sake.

(4.) The mouth-organs must assume exactly the same position when the bee bores into delicate tissues by means of the sharp points of its laminae; whether to secure the sap, as in the case of our orchids which secrete no free honey, or to reach deeply-placed honey through the aperture, as, for example, *Bombus terrestris* does in the case of meadow-clover and many other long-tubed flowers.

(5.) In collecting pollen, hive-bees and humble-bees use their mouth-parts in two different ways to moisten it, according as it is the fixed pollen of entomophilous, or the loose, easily scattered pollen of anemophilous flowers. In the former case (*e.g.* when *Apis mellifica* collects pollen on *Salix*), the bee has its suctorial apparatus completely folded down (as in Fig. 21), bringing the mouth-opening, which lies between the base of the mandibles and the labrum, close over the pollen. The bee ejects a little honey on the pollen, and then takes it up by means of its tarsal brushes and places it in the baskets on the tibiae of its hindlegs; it often makes use of its mandibles to free the pollen, before moistening it with honey. In the latter case, which I have observed in *Plantago lanceolata* and which will be fully described in my account of that plant, the bee, hovering over the flower, ejects a little honey upon the anthers from its suction-tube, which is fully extended but completely sheathes the tongue. In this case, therefore, as when alighting to suck upon a flower or when boring into soft tissues, the base of the tongue is contained within the hollow of the mentum, and the retractors are directed backwards. Since hive-bees and humble-bees on entomophilous flowers suck honey with outstretched proboscis and collect pollen with it folded up, and on anemophilous flowers collect pollen only, it follows that they can never suck honey and gather pollen simultaneously; they must always do first one and then the other, and since the pollen has to be moistened with honey, the act of sucking must always be the first.

But all forms of bees which collect dry pollen among their feathery collecting-hairs, may, so far as the structure of the flower permits, gather pollen and suck honey at the same time, and they perform the latter action in exactly the same way as hive-bees and humble-bees do. Bees with abdominal collecting-apparatus may with the greatest ease perform both acts together on flowers which present their pollen from below.

(6.) Finally, to place the mouth-parts in a position of rest, or to make use of the mandibles, the bee brings all the four

Method  
moistening  
pollen

folding movements which its suction apparatus is capable of into play simultaneously. It draws back the base of the tongue into the hollow end of the mentum (as in Fig. 20); folds the tongue, together with the inclosing laminæ and labial palps, downwards and backwards (Fig. 20 shows this action beginning), draws the retractors (*z*) backwards (half completed in Fig. 20), and rotates the cardines *c* (which in the figure are still directed obliquely forwards), backwards; the whole apparatus is thus folded together, and lodged in the cavity below the head, completely filling it (Fig. 21, 1).

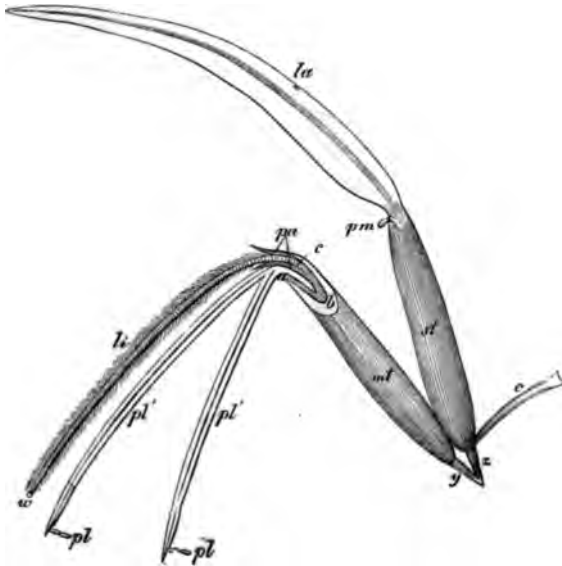


FIG. 20.—Sucking apparatus of *Bombus silvarum*, L., half folded up. Side view.

The outer wall of the hollow end of the mentum is broken away to show the involution of the lowest piece of the tongue, *abc*.

Letters as in Fig. 18,—except: *a*, base of tongue; *b*, angle of fold; *abc*, part of tongue folded in mentum.

When the hive-bees and humble-bees were declared to be the most important of all insects in the fertilisation of our native flowers, this assertion applied only to the individuals concerned in the care of the young, *i.e.* the workers among the hive-bees, and the females and workers among the humble-bees.

In all species which provide for their own young, the males are of much less use in fertilising plants than the females, as they only look after their own maintenance, and accordingly neither collect pollen nor visit flowers very diligently. Yet in all species in

which a more or less thick coat of feathery hairs has become developed upon the bodies of the females, it has become transmitted by inheritance to the males also,<sup>1</sup> so that they in their visits to flowers collect pollen as well as the females. It is otherwise with the majority of those bees which have acquired the habit of not gathering pollen themselves to feed their young, but of laying their eggs in the nests of other bees already stored with food. Some of these "cuckoo-bees," which have acquired the habit in comparatively recent times, as the parasitic humble-bees (*Apathus* or *Psithyrus*), have almost the same development of hairs as their parent-form; others which acquired it earlier, as *Nomada*, *Epeolus*,

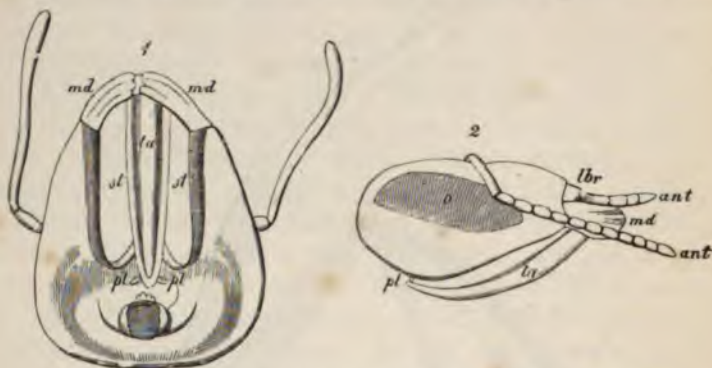


FIG. 21.—Mouth-parts of a Humble-bee (*B. hortorum*, ♂) in retracted condition.

1.—Head seen from below.

2.—Head, in side view, with proboscis bent slightly downwards. *ant*, antennae; other letters as in Fig. 18.

*Celioxys*, and *Stelis*, have almost entirely lost the hairy coat, while retaining in perfection the suctorial apparatus which furnishes them with their own food. Males and females of these "cuckoo-bees" thus plunder flowers of their honey, like the males of the hairy bees, without being of corresponding advantage to the flowers in the carriage of pollen; for only very little pollen adheres to their naked or almost naked chitinous bodies.<sup>2</sup>

<sup>1</sup> For a further account of this hereditary transmission, see my work No. 613.

<sup>2</sup> I have investigated the actions of male bees and of cuckoo-bees in regard to flowers, and embodied my results in my essays, "Die Entwicklung der Blumenthätigkeit der Insekten," and "Verschiedene Blumenthätigkeit der Männchen und Weibchen" (*Kosmos*, ix. pp. 351—370, 415—432. 1882.)

### Lepidoptera.

If the chief divisions of insects are to be arranged in the order of their importance as fertilisers of our native flowers, the first place must decidedly be given to bees,—while the Lepidoptera take only the second or third place, before or after the Flies. But if, as here, we base our arrangement on the degrees of adaptation to flowers, they undoubtedly take the first place, as the only order which throughout, and not only in certain of its families, is fitted for obtaining honey.

In the perfect state, butterflies, so far as they take food at all, which is not the case in all species, restrict themselves almost entirely to honey; and since they take no further thought for their young than to lay their eggs sufficiently concealed upon the food-plant, their mouth-parts have been quite free to adapt themselves to the easy winning of honey from the most various flowers. This adaptation is attained by an astonishing development of the maxillary laminæ, with suppression of the greater part of the rest of the mouth-organs. The upper lip, or labrum (*lbr*, 2, Fig. 22), and mandibles (*md*) are aborted. The laminæ of the maxillæ are transformed into two immensely long, hollow, rounded filaments, provided with semicircular grooves on their inner surfaces, and so forming a tube when placed in close apposition; in the state of rest this tube is spirally coiled, and concealed between the labial palps. The maxillary palps, which are not visible in my figure, and also the labium, are usually more or less abortive. The whole mechanism of the mouth, so complex and many-jointed in bees, is thus here reduced to a long, thin, suctorial tube formed of two apposed grooves and capable of being rolled up into small space, and of a protective covering for this tube.

With this simple mechanism, Lepidoptera are able to probe the most various flowers, whether flat or long and tubular, and to secure their honey. Peculiar stiff, sharp-pointed appendages at the ends of the laminæ (5, Fig. 22) enable them also to tear open delicate succulent tissues, and make use of the sap in flowers which secrete no free honey (cf. *Cytisus Laburnum*, *Erythraa Centaurium*, *Carum*, etc.). At the Cape of Good Hope, Lepidoptera do damage to plums and peaches by piercing their skins in this manner.<sup>1</sup> In Queensland also, the oranges are injured by a nocturnal form, *Ophideres fullonica*, the powerful teeth on whose

<sup>1</sup> *Ann. and Mag. of N. H.*, September, 1869.

proboscis are figured and described by M. Kunkel,<sup>1</sup> Francis Darwin,<sup>2</sup> Reginald Bligh Read,<sup>3</sup> and W. Breitenbach.<sup>4</sup> My brother Fritz Müller thinks that some of the appendages of the proboscis in Lepidoptera may be organs of touch or taste. These, which differ much in number, size, and form in different species, are usually somewhat movable, and bear at their tips a delicate rod, resembling the tactile rods or olfactory hairs of Crustacea, etc. Among the forms in which these have been noted are *Prepona Laertes*, *Hesperocharis Erotia*, *Colænis Julia*, *Apatura Hübneri*.



FIG. 22.—Adaptive modifications in Lepidoptera.

- 1.—Head of *Polyommatus Phlaeas*, L., with proboscis half unrolled.
- 2.—Head of *Vanessa Io*, L., after both laminae of the maxillae and the labial palps have been cut away at their bases ( $\times 7$ ).
- 3.—Part of the lamina of *Macroglossa fuciformis*, L., seen from within; more highly magnified. *a*, channel.
- 4.—Transverse section of the apposed laminae of the same insect, equally magnified. *aa*, tube formed by apposition of the two channels.
- 5.—Point of lamina of *Vanessa Atalanta*, L.

Lettering in 2 as in Fig. 11.

In regard to their length, the maxillary laminae of our Lepidoptera show all degrees, from the proboscis of the *Convolvulus* Hawk-moth, 80 mm. long, to a proboscis scarcely a millimetre long. Their mouth-organs may be almost entirely abortive and only comparable to those of the *Phryganidae*, pointing to these as

<sup>1</sup> *Comptes Rendus*, August 30, 1875.

<sup>2</sup> *Q. J. Micros. Sci.* vol. xv. N.S., pp. 385—390.

<sup>3</sup> *Proc. Linn. Soc. N. S. Wales*, August, 1878.

<sup>4</sup> *Archiv. f. Micr. Anat.* Bd. xiv. pp. 308—317. Breitenbach has since published some further studies on the boring apparatus of Lepidoptera (*ibid.*, Bd. xv. pp. 8—19; *Entomol. Nachrichten*, September 15, 1879, and February 15, 1880).

the ancestors of the Lepidoptera. In a former work<sup>1</sup> I have sought to establish the pedigree of Lepidoptera, which has been foreshadowed by entomologists since last century: the subject has been much more thoroughly discussed by my friend Dr. A. Speyer,<sup>2</sup> by Mr. R. MacLachlan,<sup>3</sup> and by my brother Fritz Müller.<sup>4</sup> Apart from tiny midges (*e.g.* the fertilisers of *Arum* and *Aristolochia*), and from those insects, especially beetles and bees, which occasionally or habitually take up their quarters for the night in flowers, Lepidoptera seem to be the only insects which do not confine their visits to flowers to the daylight: a large number of their species have acquired the habit of seeking their honey in the dusk of summer nights and evenings, free from the competition of other insects.<sup>5</sup> But in our climate, summer evenings on which twilight-loving and nocturnal Lepidoptera fly abundantly are not very numerous. Though the swift and violent movements of these species may be due to the shortness of the period suitable for their flight, or to the pursuit of bats, this peculiarity is of very great importance to the plants they visit; for the more flowers will be visited in a given time, the less time that is spent on each, and the shorter the time that is spent in the flight from one to another. This explains how many flowers have adapted themselves specially to nocturnal insects, both by their light colours, visible in the dusk, and by their time of opening, of secreting honey, or of emitting their odour. The Sphingidæ perform their work as fertilisers peculiarly rapidly, dropping their long proboscis into a flower while hovering over it, and instantly hastening away on their violent flight to another. Accordingly most nocturnal flowers have adapted themselves specially to these Lepidoptera, hiding their honey in such deep tubes or spurs that it is only accessible to the Sphingidæ.

<sup>1</sup> *Verh. des naturh. Vereins f. pr. Rheinland und Westfalen*, 1869, "Correspondenzblatt," pp. 57—63.

<sup>2</sup> *Stettiner Entom. Zeitung*, 1869, pp. 202—223.

<sup>3</sup> *J. Linn. Soc., Zool.*, vol. xi. p. 100.

<sup>4</sup> *Kosmos*, vol. iv. pp. 388—390.

<sup>5</sup> In South Brazil, according to my brother Fritz Müller, a social wasp, *Apocica pallida*, Lep., seeks honey only by night, sitting still in its nest by day.

### PART III.

#### THE MECHANISMS OF FLOWERS.

In this section I propose to discuss such questions as the following, in regard to a number of native or commonly cultivated plants. By what insects is each visited? What does the insect come in quest of, and how does it behave? In what manner does it effect transference of the pollen? What peculiarities of the flower have special relation to the particular visitors? What special peculiarities of the flower aid cross-fertilisation in case of insect-visits? In absence of insects, can self-fertilisation take place, and to what extent does it actually occur?

There are few instances in which I am in a position to answer all these questions. In some cases I have studied the structure of the flower but have never had an opportunity of observing its insect-visitors; in other cases I have noted insect-visitors without studying closely the mechanism of the flower.

In choosing my figures I have taken account of those already existing. In many cases I have omitted to figure flowers which happen to be well illustrated in the works of Sprengel, Darwin, or Hildebrand (*e.g.* *Aristolochia Clematidis*, *Viola tricolor*); in other cases I have selected a different species of the genus (*e.g.* *Iris*, *Polygala*). And in most cases I have passed over with a few words flowers which have been described elsewhere in great detail, unless I had to correct or amplify the previous accounts.

Professor Schenck of Weilburg has checked my identifications of the greater part of my bees, wasps, and sand-wasps (*fossoræ*); Mr. Frederick Smith has compared all my species of bees, wasps, and sand-wasps with the collection in the British Museum (which includes Kirby's type-specimens); Dr. Speyer of Rhoden has placed my determinations of Lepidoptera beyond dispute, and Herr Winnertz of Crefeld has identified those Diptera concerning which I remained doubtful. Herr Borgstette, jun., of Teklenburg, has sent me numerous insects collected upon flowers in his neighbourhood, along with accurate records of the plant on which each specimen was obtained.

#### *Contractions employed in the Lists of Insects.*

l.h.=licking honey; s.=sucking; c.p.=collecting pollen; f.p.=feeding on pollen; cor.=corolla; ab.=abundant.

Sld. = Sauerland (Warstein, Möhnethal, Brilon); Tekl. = Teklenburg (Herr Borgstette); Th. = Thuringia (neighbourhood of Mühlberg). In all cases in which the locality is not specially mentioned, the observation was made near Lippstadt.

Numbers placed in brackets after the names of insects indicate the length of the proboscis in millimetres.

♂ = male; ♀ = female; ♀ = worker.

#### ORD. *RANUNCULACEÆ*.

1. *CLEMATIS RECTA*, L.—The flowers are destitute of honey. When they open, the stigmas are still immature, and are covered up partly by the stiff hairs of the pistil, and still more efficiently by the stamens which press closely upon them. The outermost of these latter soon begin to bend outwards, and their narrow anthers dehisce lengthwise, so that the broad connectives appear covered on both sides with pollen. At this time, the flowers are well fitted to supply pollen to insects, but the stigmas are unable to retain pollen with which the insect-visitors are coated. The bending outwards and dehiscence of the anthers now proceeds centripetally, and before the innermost stamens have joined the rest the stigmas lie fully developed in the middle of the flower. Insects which come at this period from other flowers and settle in the middle must accomplish cross-fertilisation. Bees almost always alight in the middle of the flower, both because they can more conveniently reach the stamens from the centre than from the edge, and also because the anthers near the centre are least likely to have been already emptied. The pollen-eating flies which settle at random on the flowers and creep about in them can produce self-fertilisation as easily as cross-fertilisation. In default of insect-visits, self-fertilisation readily takes place, for the outermost stigmas are often touched by pollen at the bursting of the anthers, and frequently part of the stigmas lie so that pollen may fall directly on them from anthers above.

Since the flowers are destitute of honey, and all attractions for insects therefore cease with the dispersal of the pollen, their protogynous condition has not been able to perfect itself. They are naturally only visited persistently by pollen-seeking insects, but by these in considerable abundance, owing to the large stock of pollen.

A. Hymenoptera—(a) *Apidae*: (1) *Prosopis signata*, Pz. ♂, f.p.; (2) *Andrena Gwynana*, K. ♀; (3) *A. albicans*, K. ♀; (4) *Halictus sexnotatus*, K. ♀; (5) *Osmia rufa*, L. ♀; (6) *Bombus terrestris*, L. ♀; (7) *Apis mellifica*, L. ♀;

(b) *Sphingidæ*: (8) *Oxybelus uniglumis*, L., f.p. *ab.*; (9) *Gorytes mystaceus*, L., hovering over the flowers, perhaps in order to plunder flies; (c) *Vespidæ*: (10) *Odynerus parietum*, L. ♀, *do.* B. Diptera—(a) *Syrphidæ*: (11) *Syrphus pyrastris*, L.; (12) *Helophilus florens*, L.; (13) *Eristalis sepulcralis*, L.; (14) *E. arbustorum*, L.; (15) *Syrphidæ pipiens*, L.; (16) *Xylota ignava*, Pz.; (17) *X. lenta*, Mgn., all f.p.; (b) *Muscidæ*: (18) *Prosenia siberita*, F. C. Coleoptera—(19) *Trichius fasciatus*, L., devouring the whole of the anthers.

In *Clematis Balearica*, Rich. (*C. cirrhosa*, L.), the outermost stamens are metamorphosed into spoon-shaped nectaries, which are sucked by *Bombus* and *Xylocopa*; in *Clematis integrifolia*, L., the inner stamens secrete honey (567, p. 8).

2. *THALICTRUM AQUILEGIFOLIUM*, L.—The stamens in this plant play the part of petals: they are of a pale lilac colour, thickened and club-shaped, and radiate outwards, forming considerable bundles, fifteen to twenty mm. in diameter. When the flower opens, the stigmas are covered over and shielded from insects by the central stamens, which are crowded together and have their anthers still closed. In young flowers the insects alight upon the anther-bearing points of the stiff filaments, and climb with some difficulty around and over them in search of pollen. In older flowers the central stamens are directed more outwards, so that now the insects can alight more conveniently upon the stigmas. Thus cross-fertilisation is accomplished. In default of insect-visits, self-fertilisation is provided for by part of the stigmas always standing in the way of falling pollen.

The flowers are devoid of honey, and are visited only by pollen-seeking insects.

A. Hymenoptera—*Apidæ*: (1) *Prosopis signata*, Pz. ♂ ♀, f.p.; (2) *Halictus sexnotatus*, K. ♀, c.p.; (3) *Apis mellifica*, L. ♂, c.p. B. Diptera—*Syrphidæ*: (4) *Rhingia rostrata*, L.; (5) *Eristalis arbustorum*, L.; (6) *E. nemorum*, L.; (7) *E. sepulcralis*, L.; (8) *E. tenax*, L., all f.p. C. Coleoptera—(9) *Trichius asciatus*, L., devouring the anthers bodily. See also No. 609, p. 125.

*Atragene alpina*, L.—The pendulous violet flowers only give up their honey to insects which can force asunder the numerous stamens, which are set closely in several whorls,—viz. bees and humble-bees; and in point of fact only these insects have been observed to fertilise the plant (590, 609). The grooved inner surface of the basal half of the filament secretes and lodges honey.

3. *THALICTRUM FLAVUM*, L.—This plant, which is abundant on meadows by the Lippe, has likewise honeyless flowers. I found

them to be chiefly visited by pollen-feeding flies, and on July 1, 1868, I took the following :—

A. Diptera—(a) *Syrphidæ*: (1) *Eristalis nemorum*, L.; (2) *E. arbustorum*, L.; (3) *E. tenax*, L.; (4) *E. sepulcralis*, L., all four f.p., very *ab.*; (5) *Syritta pipiens*, L., f.p.; (b) *Muscidæ*: (6) *Pollenia Vespillo*, F., f.p., *ab.* B. Hymenoptera—*Apidæ*: (7) *Apis mellifica*, L. ♀, c.p., very *ab.*

*Thalictrum minus*, L., is an anemophilous descendant of entomophilous ancestors. The flowers are proterogynous, and retain, as traces of their former entomophilous condition,—the non-simultaneous dehiscence of the anthers, slight cohesiveness of the pollen, and perhaps also the conspicuous yellow colour of the anthers (590, 1.).

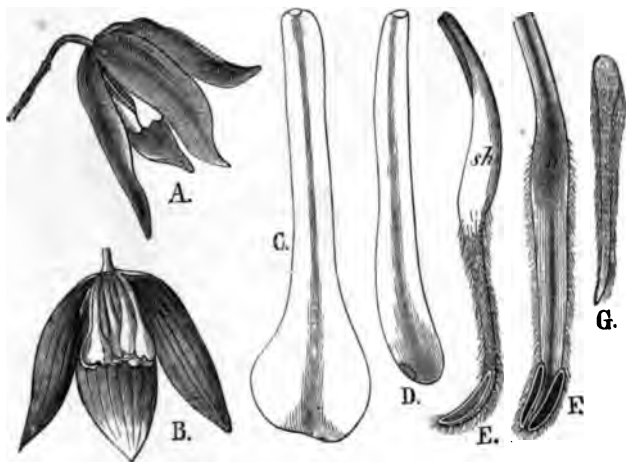


FIG. 23.—*Atragene alpina*, L.

- A.—Flower in side view,  $\times 3$ .  
 B.—Ditto, after removal of one sepal.  
 C.—One of the four large petals.  
 D.—One of the inner small petals, with a rudimentary anther-lobe at one side (C and D seen from the inside).  
 E.—Stamen in side view.  
 F.—Ditto, seen obliquely from within.  
 G.—A carpel (C—G,  $\times 43$ ).  
 n, nectary; sh, honey-receptacle.

*Hepatica triloba*, Gil. (*Anemone hepatica*, L.), is visited by bees and *Syrphidæ* for its pollen (590, 1.).

*Pulsatilla vulgaris*, Mill. (*Anemone Pulsatilla*, L.).—The abundant pollen is much sought by bees; honey is secreted by rudimentary stamens reduced to short stalked knobs (590, 1.).

*Pulsatilla vernalis*, L.—My specimens from the Stelvio were slightly proterogynous; Ricca's, from Val Camonica, were very markedly so. The nectaries here also are modified stamens (590, 609).

4. *ANEMONE NEMOROSA*, L.—This plant also has flowers destitute of honey, in which, however, the sepals, not the stamens, play the part of petals in rendering the flower conspicuous. When the flowers open, the stigmas are still covered up and protected by the stamens, but during the greater part of the period of flowering both stigmas and anthers are mature at the same time, and exposed to the touch of insects. These alight sometimes in the centre of a flower, sometimes on a sepal, touching, therefore, either stigmas or anthers first, and they accomplish self-fertilisation as well as cross-fertilisation. The inclined position of the flower brings more or

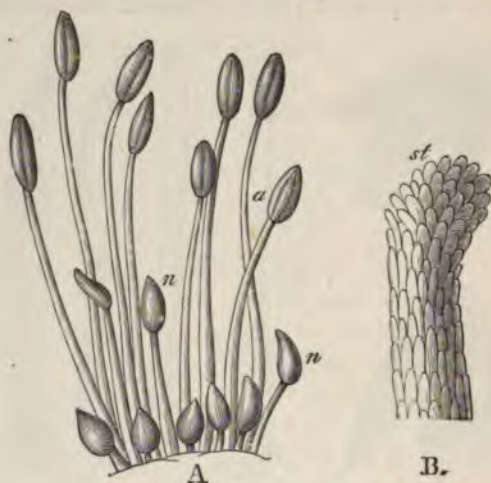


FIG. 24.—*Pulsatilla vernalis*, L.

A.—Some of the outermost stamens metamorphosed into nectaries; and some of the next in order, which retain their proper function. ( $\times 7$ )

B.—Top of style, with the stigma, more magnified.

less of the stigmas in the line of fall of the pollen, which leads to self-fertilisation if insects' visits fail; but experiment has yet to decide on the efficacy of this self-fertilisation.

On February 25, 1868, out of seven flowers in my room, which had opened simultaneously, I fertilised two with pollen from other flowers, two with their own, and I left three untouched. On February 29, in both of those which had received the pollen of other flowers, all the anthers had fallen off and the ovaries were distinctly swollen; in the two which had been fertilised with their own pollen, most of the anthers had fallen off and the ovaries were swollen, but much less so than in the two former cases; the three remaining flowers, which had been untouched, still retained all

their anthers. The sepals were still quite fresh in all seven flowers. The experiment was not completed, as the plants withered in the irregularly-heated room.

Visitors : A. Hymenoptera—(1) *Halictus cylindricus*, F. ♀, c.p. ; (2) *Andrena fulvicrus*, K. ♀, c.p. ; (3) *A. albicans*, K. ♂, f.p. ; (4) *Osmia fusca*, Christ. ♀, c.p. ; (5) *Apis mellifica*, L. ♀, in hundreds, c.p. and also s. B. Diptera—(6) *Scatophaga stercoraria*, L. ; (7) *Sc. merdaria*, F., both f.p. C. Coleoptera—(8) *Meligethes*, f.p. ; (9) *Mordella pumila*, Gyll. See also 590, I.

Although I could not detect any honey, even by help of a lens, I repeatedly observed a hive-bee flying from flower to flower and thrusting its proboscis into one or more spots in the base of the flower, between the sepals and carpels. Here the bees doubtless tapped the juice which the flowers did not of themselves furnish, and which the bees were in want of to moisten the pollen that they collected at the same time. Once I saw a honey-bee first suck honey on flowers of *Cardamine pratensis* and then fly off to gather pollen on *Anemone nemorosa*.

Even in spots where *Primula elatior* was blooming abundantly, hive-bees remained busily occupied upon the wood anemone.

*Anemone alpina*, L.—This species is androdioecious. The male flowers are distinctly smaller than the hermaphrodite, and the latter are proterogynous. The plant is visited by numerous bees and flies, though the flowers are devoid of honey (609).

*Anemone narcissifolia*, L., is proterandrous, the stigmas not being mature until the anthers have dehisced or have even been emptied. The flowers are devoid of honey (609).

*Adonis vernalis*, L., is proterogynous and devoid of honey. The visitors are chiefly bees and also ants (590, I.).

*Myosurus minimus*, L., is proterandrous, according to Delpino. After the anthers wither, the apex of the ovary becomes lengthened into a long cone and develops its stigmas. Delpino thinks that the flowers are fertilised by flies (No. 177, p. 57).

According to my own observations, the enormous elongation of the axis bearing the pistil has simply the object of self-fertilising most of the numerous stigmas by means of the small number of anthers, for insect-visitors are very few. The anthers, which lie close around the axis, let their pollen emerge very gradually by two lateral slits, while the lengthening axis brings fresh stigmas in contact with them. As visitors of this plant, I have observed chiefly minute insects, not more than 1 to 1½ mm. long, viz. Diptera of the genera *Sciara*, *Chironomus*, *Scatopse*, *Phora*, *Cecidomyia*,

*Oscinis*, and *Microphorus*, besides small *Pteromalidæ* and minute *Ichneumonidæ*, a small *Haltica*, some *Anthomyiæ*, and a single *Melanostoma mellina* (570, vol. x. p. 129).

5. *RANUNCULUS AQUATILIS*, L.—The yellowish base of each petal serves to guide insects towards the honey; on it stands an obliquely-placed tubercle, truncate above, and provided with a honey-secreting hollow, which plays the parts of gland and receptacle for the nectar.

The anthers, which are few in number, dehisce one after the other when the flower opens, and cover themselves all round with pollen; the stigmas become developed at the same time, and often come in contact spontaneously with the pollen on the anthers.

The flowers are frequented by a large number of insects, especially *Diptera*, which alight sometimes in the middle of the flower, sometimes on the edge, and so effect self-fertilisation as well as cross-fertilisation.

A. *Diptera*—(a) *Syrphidæ*: (1) *Eristalis tenax*, L.; (2) *E. arbustorum*, L.; (3) *E. nemorum*, L., all three abundant, now sucking, now collecting pollen, plentifully dusted with pollen on the legs and especially on the soles of the feet; (4) *Helophilus florens*, L.; (5) *Chrysogaster viduata*, L., also s. and f.p.; (b) *Muscidæ*: (6) *Scatophaga merdaria*, F., f.p.; various small *Muscidæ*, s. and c.p. which escaped me. B. *Hymenoptera*—*Apidæ*: (7) *Apis mellifica*, L. ♀, ab., s. and c.p.; (8) *Bombus terrestris*, L. ♀, s. C. *Coleoptera*—*Chrysomelidæ*: (9) *Helodes phellandrii*, L., devouring anthers and petals. See also No. 590, I., pp. 48, 49.

When the water is unusually high, the flowers of *Ranunculus aquatilis* remain submerged and do not open, but fertilise themselves (17, p. 14, 351, p. 17).

*Ranunculus glacialis*, L., is slightly proterandrous (Ricca); *R. alpestris*, L., is homogamous or slightly proterogynous; *R. parnassifolius*, L., and *R. pyrenæus*, L., var. *bupleurifolius*, D.C., are proterogynous with persistent stigmas. In all these species the shape of the nectaries is very variable (609).

6. *RANUNCULUS FLAMMULA*, L.—The flowers have scarcely opened when the outermost anthers dehisce extrorsely, covering their sides which are turned towards the petals with pollen, so that insects which try to plunder the honey secreted by the little scales at the base of the petals must of necessity dust themselves with pollen. The stigmas are at this time concealed or almost concealed by the inner stamens, and so are ensured against contact with insects; they are, moreover, not yet fully developed. The

opening of the anthers progresses slowly towards the centre of the flowers, and each stamen as it dehisces bends outwards and turns its pollen-covered side outwards. These stigmas are fully developed before the *innermost* stamens join the others, and the flowers, which before could only dust their visitors with pollen, can henceforth be fertilised either with their own or other pollen. All visitors which alight, bearing pollen, in the middle of the flower effect cross-fertilisation; others, which alight first on a petal and

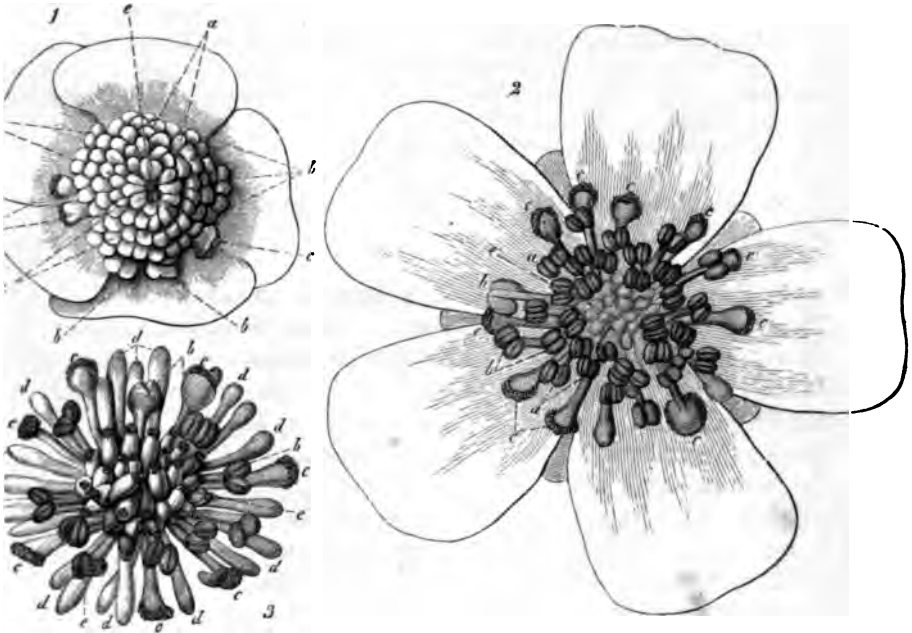


FIG. 25.—*Ranunculus Flammula*, L.

- 1.—Flower just opening.
  - 2.—Flower in which the stamens are fully developed, the stigma still immature.
  - 3.—Essential organs of a flower in which the stigmas are fully mature, and the anthers are not yet withered.
- a, immature anthers; b, anthers about to dehisce; c, ditto, dehiscent; d, ditto, empty; e, carpel.

touch the anthers and then the stigmas, can accomplish either self-fertilisation or cross-fertilisation. So if insects alight in equal numbers in the two ways, cross-fertilisation must be the more frequent result. After numerous observations on this and the following species of *Ranunculus*, I am able to state that the two modes of alighting are equally common for small insects; but all larger insects (which are about as long as the diameter of the flower) come in contact with the stigmas and the anthers at the

same time, and therefore must dust the stigmas with pollen from other flowers; hence the cross-fertilisations are still more numerous than the self-fertilisations. In default of insect-visits, the power of self-fertilisation is retained, some of the outermost stigmas being often touched by pollen from the innermost anthers.

Although the arrangement of the flower is quite like that of the following species of *Ranunculus*, *R. Flammula* is very sparingly visited by insects, one reason at least being that its flowers are much smaller and less conspicuous.

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Syritta pipiens*, L., c.p. and s. (2) *Cheilosia*, sp. f.p.; (3) *Melithreptus tæniatus*, Mgn., f.p. and s.; (b) *Muscidæ*: (4) *Scatophaga merdaria*, F., f.p.; (5) *Anthomyia* sp. B. Hymenoptera—*Apidæ*: (6) *Halictus cylindricus*, F. ♀, c.p.; (7) *H. flavipes* F. ♀, c.p. C. Lepidoptera—(8) *Satyrus pamphilus*, L., s.

*Ranunculus montanus*, L., is proterogynous with persistent stigmas (609).

7. *RANUNCULUS ACRIS*, L., *R. REPENS*, L., *R. BULBOSUS*, L.—These species agree with *R. Flammula* in the structure of their flowers, and with each other in their habitat, in the conspicuousness of their flowers, and therefore also in the insects which visit them. Mr. Thomas Whitelegge (No. 774) states that they are all sometimes gynodioecious. I have observed very many of the following visitants in equal abundance and similarly engaged on all these species; and I have even noticed the hive-bee, which in general keeps strictly to one species of flower, pass from *Ranunculus acris* to *R. repens* and *R. bulbosus*, or *vice versâ*, without any distinction. I accordingly catalogue the visitors of these three species together.

A. Diptera—(a) *Empidæ*: (1) *Empis tessellata*, F., s.; (b) *Asilidæ*: (2) *Dioctria atricapilla*, Mgn. (Tekl. B.); (c) *Syrphidæ*: (3) *Chrysotoxum arcuatum*, L. (Sld.), s. and f.p.; (4) *Chr. festivum*, L., s.; (5) *Pipiza funebris*, Mgn., s.; (6) *P. chalybeata*, Mgn., f.p.; (7) *Chrysogaster Macquarti*, Loew.; (8) *Ch. viduata*, L., very ab., both s. and f.p.; (9) *Cheilosia pubera*, Zett., f.p., ab.; (10) *Ch. albitarsis*, Mgn., ab., s. and f.p.; (11) *Melanostoma mellina*, L., s.; (12) *Platycheirus albimanus*, F. (Tekl. B), f.p.; (13) *Syrphus ribesii*, L.; (14) *Eristalis tenax*, L.; (15) *E. arbustorum*, L.; (16) *E. nemorum*, L.; (17) *E. sepulcralis*, L.; (18) *Melithreptus scriptus*, L.; (19) *M. pictus*, Mgn.; (20) *M. tæniatus*, Mgn.; (21) *Syritta pipiens*, L.,—the last nine ab., both s. and f.p.; (d) *Muscidæ*: (22) *Cyrtoneura cærulescens*, Mcq., s.; (23) *Anthomyia*, sp. B. Coleoptera—(a) *Nitidulidæ*: (24) *Meligethes*, very ab., s. and f.p.; (b) *Dermestidæ*: (25) *Byturus fumatus*, F., f.p., ab.; (c) *Buprestidæ*: (26) *Anthaxia nitidula*, L. in copulâ on flowers of *R. repens*; (d) *Mordellidæ*: (27) *Mordella aculeata*, L.; (28) *M. pusilla*, Dej.; (29) *M.*

pumila, Gyll.; (e) *Ædemeridæ*: (30) *Ædemera virescens*, L., ab.; (f) *Cistelidæ*: (31) *Cistela murina*, L., devouring the petals and stamens; (g) *Cerambycidæ*: (32) *Strangalia nigra*, L., do.; (h) *Chrysomelidæ*: (33) *Helodes aucta*, F., devouring the petals, along with its larvæ (May 24, 1870); (34) *Cryptocephalus sericeus*, L., devouring the anthers. C. Hymenoptera,—(a) *Tenthredinidæ*: (35) *Cephus spinipes*, Pz., ab., s. and devouring the anthers; (36) *Cephus*, small undetermined species; (b) *Sphegidæ*: (37) *Oxybelus uniglumis*, L.; (c) *Vespidæ*: (38) *Odynerus spinipes*, H. Sch. ♀ (quinquefasciatus, F.); (d) *Apidæ*: (39) *Prosopis hyalinata*, Sm. ♂, s. and f.p.; (40) *Halictus longulus*, Sm. ♀, s.; (41) *H. flavipes*, F. ♀, c.p.; (42) *H. villosulus*, K. ♀; (43) *H. sexsignatus*, Schenck, ♀, s.; (44) *H. rubicundus*, Chr. ♀, s.; (45) *H. quadricinctus*, F. ♀, c.p.; (46) *H. leucozonius*, Schr. ♀, laden with pollen, sheltering itself from the rain in flowers of *R. bulbosus* (June 10, 1871); (47) *H. zonulus*, Sm. ♂, s.; (48) *H. cylindricus*, F. ♀, c.p.; (49) *H. maculatus* Sm. ♀ ♂, s. and c.p., ab.; (50) *H. nitidiusculus*, K. ♀, s.; (51) *H. sexnotatus*, K. ♀, c.p. and s.; (52) *Andrena fulvicrus*, K. ♀ ♂, s. and c.p., ab.; (53) *A. albicans*, K. ♀ ♂, do.; (54) *A. albicus*, K. ♂, s.; (55) *Panurgus calcaratus* Scop., s.; (56) *Chelostoma florissomne*, L. ♀ ♂, c.p. and s.; (57) *Osmia rufa*, L. ♂, s.; (58) *Apis mellifica*, L. ♀, s. D. Lepidoptera—(59) *Lycæna icarus*, Rott.; (60) *Satyrus pamphilus*, L.; (61) *Polyommatus Phlœas*, L.; (62) *Euclidiaglyphica*, L., all s. See also No. 590, 1., pp. 49—59; No. 609, p. 135.

If we compare the insect-visitors of these species of *Ranunculus* with those of the typical Umbelliferæ, we observe the following remarkable differences. (1) Since the honey lies less exposed, those insects which are least fitted for sucking flowers are absent, viz. *Neuroptera*, *Ichneumonidæ*, *Tipulidæ*, etc.; *Sphegidæ* and *Vespidæ* are only met with sparingly. (2) Of the flies, *Syrphidæ* form the great majority; they are fond of brilliant colours, and are attracted by the bright yellow of the *Ranunculus* flowers. (This love of colours is clearly expressed in their own colours, the result of sexual selection.) (3) It is also owing to their bright colour that the flowers are frequented by the beetle *Cryptocephalus sericeus*, and that *Anthaxia nitidula* resorts to them for pairing. In these and in many other beetles, as in the humble-bees, it seems as if the habit of feeding on flowers had called out the colour-sense and the taste for bright colours, and that sexual selection had then been guided by this taste. (4) Bees occur much more abundantly on flowers of *Ranunculus* than on the Umbelliferæ, because the former are richer in both honey and pollen. These flowers seem especially to meet the wants of the genus *Halictus*, of which I have taken twelve species on them, mostly in abundance. Besides the least specialised bees (*Prosopis*, *Halictus*, *Andrena*) and the most specialised (*Apis*), intermediate genera, such as *Panurgus* and *Chelostoma*, which are absent from Umbelliferæ, visit the flowers of *Ranunculus*.

8. *RANUNCULUS LANUGINOSUS*, L., is precisely similar in the arrangement of its flowers to the three last-named species: but growing in woods, where fewer flower-visiting insects occur, it is frequented by a smaller number of species in spite of its larger and more conspicuous flowers.

Visitors: A. Diptera—(a) *Empidæ*: (1) *Empis livida*, L., s.; (b) *Syrphidæ*: (2) species of *Cheilosia*, f.p., ab.; (c) *Muscidæ*: (3) *Anthomyia*, f.p., very ab. B. Coleoptera—(a) *Nitidulidæ*: (4) *Meligethes æneus*, F., ab. (I could see distinctly with a lens how these small beetles gnawed the inner surface of the petals and the stamens); (b) *Dermestidæ*: (5) *Byturus fumatus*, L., f.p., ab. C. Hymenoptera—(a) *Tenthredinidæ*: (6) *Cephus pallipes*, Kl., very ab., f.p. and s., along with other species; (b) *Apidæ*: (7) *Andrena cingulata*, F. ♀, c.p.; (8) *Chelostoma florissomne*, L. ♂, s.; (9) *Osmia fusca*, Christ. ♀, c.p., and at the same turning round in the flower and emptying all the nectaries; (10) *Bombus terrestris*, L. ♀, s. See also No. 590, I., p. 51.

9. *RANUNCULUS FICARIA*, L., also resembles *R. acris*, *R. repens*, and *R. bulbosus*, but it blooms earlier when fewer flower-visiting insects are abroad, a disadvantage which is perhaps partly compensated for, by the insects having at that time fewer kinds of flowers to choose from. At the beginning of the flowering period, we find as in *R. auricomus*, many flowers with very few petals, sometimes so few as two or three: later on the number increases to eight or even eleven, and they expand in the sunshine to a golden star 20 to 25 mm. in diameter.

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Brachypalpus valgus*, Pz., f.p.; (b) *Muscidæ*: (2) *Sepsis*, ab.; (3) *Anthomyia radicum*, L., very ab.; (4) *Scatophaga merdaria*, F. B. Hymenoptera—*Apidæ*: (5) *Apis mellifica*, L., ♀, s. and f.p., ab.; (6) *Andrena Gwynana*, K. ♀, c.p.; (7) *A. albicans*, K. ♀ ♂, c.p. and s.; (8) *A. parvula*, K. ♀, s.; (9) *Halictus cylindricus*, F. ♀, s.; (10) *H. albipes*, F. ♀, s.; (11) *H. lucidus*, Schenck, ♀, s.; (12) *H. nitidiusculus*, K. ♀, s. C. Coleoptera—(13) *Meligethes*, ab., s., f.p., and gnawing the petals. D. Thysanoptera—(14) Thrips, very ab. See also No. 590, I., pp. 51, 52.

10. *RANUNCULUS AURICOMUS*, L.—The flowers of this species exhibit in their petals a great variety of forms of nectary, which are very remarkable and help us to explain the various nectaries of different *Ranunculaceæ*.

The corolla is seldom regular, but as a rule, some or even all of the petals are more or less stunted or even absent, and the sepals, with their bright yellow limb, take the place of petals partly or completely. The honey-glands at the base of the petals are subject to the following modifications. In the most perfect petals (1 and 2, Fig. 26) the inner side of the triangular claw has

usually a thickened border on either side: and these borders fuse below, and at their junction form a little pit which secretes honey. Some perfectly formed petals occur, however, in which the honey is secreted not by this hollow, but by two smaller pits which stand to the right and left, on the broader thickened margins (3, Fig. 26). In very stunted petals (5 to 7 mm. long, and 3 to 4 mm. broad,) there is developed upon the inner side of the base a smaller lamina, which is fused with the larger for the space of 2 to 3 mm., and has a free portion 1 to 3 mm. long. Between the two laminæ, two honey-canals, separated by a fold, are deeply sunk (7, 8, Fig. 26). Such petals have a striking resemblance to those of

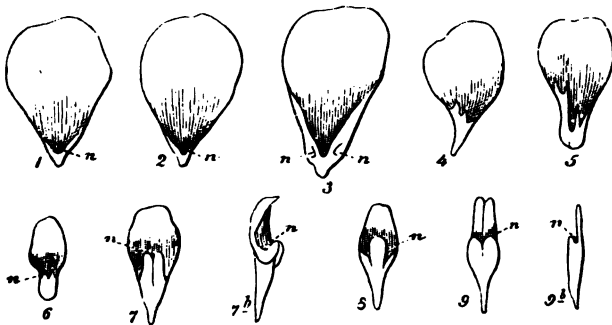


FIG. 26.

1-8.—Petals of *Ranunculus auricomus*.9.—Petal of *Eranthis hiemalis*. n, nectary.

*Eranthis hiemalis*. Between these three varieties we find various, often unsymmetrical, intermediate forms, (4, 5, 6, Fig. 26) in which sometimes no honey is secreted (4, 5).

After completion of my manuscript I found (April 5 and 20, 1872) the following insects in flowers of *R. auricomus*: A. Hymenoptera—(a) *Apidae*: (1) *Andrena parvula*, K. ♀, c.p.; (2) *A. fulvescens*, Sm. ♂, a.; (3) *Halictus cyllindricus*, F. ♀, c.p.; (b) *Formicidæ*: (4) an undetermined sp., licking honey. B. Diptera—(a) *Syrphidæ*: (5) *Pipizella virens*, F., f.p.; (6) *Cheilosia vernalis*, Fallen, f.p.; (b) *Muscidæ*: (7) *Anthomyia radicum*, Mgn. ♀ ♂, very ab., but so wild that I could not see what it was doing; (8) *Scatophaga merdaria*, F., a. and f.p. C. Thysanoptera—(9) Thrips, ab. Ants and Thrips were observed in the flowers by Sprengel. See also No. 590, i., p. 52.

11. *CALTHA PALUSTRIS*, L.—The honey is secreted by two shallow depressions on the sides of each carpel, bounded by a slight fold. It is so abundant that the drops secreted by the adjacent sides of two neighbouring carpels often flow together into a large drop filling up the cleft between. Anthers and stigmas ripen

simultaneously, but cross-fertilisation is favoured by the fact that, as in *Ranunculus*, the anthers open outwards, and the outermost are the first to dehisce. Self-fertilisation as in *Ranunculus* is still possible. The very conspicuous golden-yellow flowers, which expand to a diameter of more than 40 mm., are visited in sunny weather by very numerous insects, of comparatively few species owing to the early time of year.

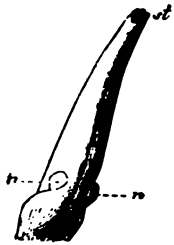


FIG. 27.—Carpel of *Caltha palustris*, L.  
st, stigma; n, nectary,  
bearing a drop of honey.

A. Diptera—(a) *Stratiomyidæ*: (1) *Odontomyia argentata*, F.; (b) *Syrphidæ*: (2) *Cheilosia* sp., f.p.; (3) *Ascia podagrica*, F., f.p.; (4) *Rhingia rostrata*, L., f.p.; (5) *Eristalis intricarius*, L. (these handsome flies displayed clearly their taste for bright colours; they hovered over the yellow flowers as the males of *Eristalis* hover over the females, then suddenly settled to suck honey or feed on pollen, and again flew off abruptly to another flower to repeat the same actions); (c) *Muscidæ*: (6) *Scatophaga merdaria*, F., f.p.; (7) *Anthomyia*, very ab., f.p. B. Coleoptera—*Nitidulidæ*: (8) *Meligethes*, very ab., s. and f.p. C. Hymenoptera—*Apidæ*: (9) *Andrena albicans*, K. ♂, s.; (10) *Osmia rufa*, L. ♂, s.; (11) *Bombus terrestris*, L. ♀, making the circuit of each flower, and licking the drops of honey from every carpel; (12) *Apis mellifica*, L. ♀, in hundreds, collecting pollen, and only sucking honey to aid in storing the pollen. See also No. 590, I., p. 52; No. 609, pp. 135, 136.

*Trollius europæus*, L., is homogamous. The stigmas are over-topped by the anthers and are dusted regularly with their pollen, which is probably outstripped in its action by pollen brought from other flowers (609).

12. *ERANTHIS HIEMALIS*, Salisb.—This, the earliest of all the *Ranunculaceæ* here considered, exhibits regularly in its petals the same conversion into little pockets for honey that our earliest species of *Ranunculus*, *R. auricomus*, displays occasionally. Its calyx has completely assumed the function of rendering the flower conspicuous, as do the sepals of *R. auricomus* to a modified extent. In other respects the arrangement of its flower agrees with those last described.

On February 26, 1871, I saw the following insects on flowers of *E. hiemalis* in my garden, during bright sunshine.

A. Diptera—*Muscidæ*: (1) *Pollenia rudis*, F., stroking petals, anthers, and sometimes stigmas, with the end-flaps of its proboscis, but finally thrusting its proboscis into the nectaries; (2) *Musca domestica*, L., ditto; (3) *Sepsis*, busy about the anthers. B. Hymenoptera—*Apidæ*: (4) *Apis mellifica*, L. ♀, s. and f.p., in great numbers, sufficient to fertilise all the flowers.

In many seasons with less favourable weather I have found *E. hiemalis* (which I have immediately in front of my window, and can easily watch) not visited by insects at all, and yet bearing fruit, but more sparingly than when insect-visits have taken place. The reason of the smaller number of seeds is that, as in *Ranunculus* and *Caltha*, self-fertilisation can only take place to a limited extent: for when I fertilised in my room, one flower with its own, and another with extraneous pollen, both produced seeds in equal abundance.

The species of *Helleborus* are proterogynous, according to Hildebrand (351).

*Nigella arvensis*, L.—The proterandrous flowers of this plant are provided with nectaries covered by movable lids, and are fertilised by bees. They have been fully described by Sprengel.<sup>1</sup>

*Nigella damascena*, L., is visited by *Ceratina callosa*, F. ♂, and *Prosopis signata*, Nyl. ♂ (Apidæ) (590, 1).

13. *AQUILEGIA VULGARIS*, L.—The five sepals of the pendulous flower form broad blue expansions, which help to render it conspicuous. Each of the five petals is hollowed out from its insertion upwards to form a hollow spur 15 to 22 mm. long, whose cup-shaped mouth is wide enough to admit the head of a humble-bee, and whose narrow tubular part curves inwards and downwards at its upper end. In this curved part is contained the honey, which is secreted by a fleshy thickening in the extreme point of the spur. Owing to its curvature the point of the spur is only 10 to 17 mm. above the insertion of the petal. To reach the honey in a legitimate way, the bees hang on to the flowers below, grasping the base of the spur with their forelegs, and holding on with their mid and hindlegs to the column formed of the stamens and carpels, which projects perpendicularly or obliquely downwards from the centre of the flower; the head, meanwhile, is introduced into the aperture of the spur, whose outer wall its upper surface touches, and the end of the proboscis follows the curvature of the spur. Since bees very easily bend the end of their proboscis downwards, but scarcely bend it voluntarily in the opposite direction, the position just described is the only one suitable for them to reach the honey. This position entails that in younger flowers the hinder and lower surface of the bee's body touch the anthers, which closely surround the carpels and which are covered on their

<sup>1</sup> See also Kerner, No. 386, p. 101, for an account of the pits in *N. sativa* and *N. elata*.

outer side with pollen; while in older flowers the same parts come in contact with the carpels which have elongated and spread their stigmas more widely apart. Cross-fertilisation is the inevitable result. Thus the Columbine is admirably adapted for fertilisation by humble-bees: but to reach the honey they must have a proboscis at least 10 to 17 mm. long, even supposing that they stick their heads fully into the mouth of the spur and so shorten the passage by about 5 mm. This fully explains the actions of the insects that I have observed on this flower. *Bombus hortorum*, L. ♀ (with a proboscis 19 to 21 mm. long), is the only insect that I have found very abundant on it; *B. agrorum*, F. ♀ (with a proboscis 12 to 15 mm. long) is found much more rarely, sucking the flowers in the regular way and accomplishing cross-fertilisation. I saw *B. terrestris*, L. ♀ (with a proboscis 7 to 9 mm. long), fly on to the upper surface of a flower, and lick over the base of the sepals, and on finding nothing there, creep to the lower surface, and thrust its head into the spur. Then it again crawled on to the upper surface, and again licked fruitlessly the base of the sepals; and finally, biting a hole in the spur at the curved part, it introduced its proboscis and plundered the honey. Without further consideration it proceeded to secure the honey of the other petals and of other flowers in the same manner. The numerous other individuals of *B. terrestris*, L. ♀, which I before and afterwards observed thus perforating the spur, had probably first learned by trial how the honey might be won.

I have often seen *B. terrestris* bite through the spurs of still unopened flowers, and so forestall all legitimate visitors. The hive-bee also, as Sprengel noticed, bites through the spur at the bend and steals the honey: it often takes advantage of the holes made by *B. terrestris*.

I have seen smaller bees, *Halictus Smeathmanellus*, K. ♀, and *H. leucozonius*, Schr. ♀, collecting pollen on these flowers, which they would naturally fertilise by doing so.

On a double garden-variety of the Columbine, in which several spurs are placed one within another, I noticed a hive-bee thrusting its head in the regular manner into the inner spur; and I could see, through the transparent flower, the tongue stretched out to its fullest extent without reaching the honey.

In default of insect-visits, self-fertilisation must easily take place, owing to the position of the parts of the flower.

*Aquilegia atrata*, Koch, is also proterandrous, and visited by humble-bees (609, p. 137).

14. DELPHINIUM ELATUM, L.—This common garden plant is marked off by the unusual function of the two whorls of the perianth from most other plants, and in part even from other species of larkspur; while it agrees with the latter in the early development of the stamens and in the peculiar movements of the stamens and stigmas.



FIG. 28.—*Delphinium elatum*, L.

- 1.—Young flower after removal of the calyx, seen from before.
  - 2.—The petals in their natural position, seen obliquely from before and below.
  - 3.—Young flower after removal of the right half of the calyx.
  - 4.—Older flower after removal of the calyx, seen from before.
  - 5.—The same flower as 3, after the right half of the corolla also has been removed.
- a a*, the two upper petals, which are prolonged backwards into two spurs, which secrete and contain honey, and which in front form an entrance for the bee's proboscis; *a'*, their bases; *b b*, the two inferior petals, whose closely approximated surfaces bound the entrance for the bee's proboscis below—on their upper surfaces, each has a tuft of yellow hairs to serve as a path-finder, while their peduncles (*b'*, 2) stand so far apart that in the first stage the anthers, in the second the stigmas, appear between them (at *b\**, 2) in the path of the insect's proboscis; *c*, anthers which have dehiscent, placed in the way of the insect's proboscis; *d*, anthers which have not yet dehiscent, bent downwards, covering the female organs; *e*, base of the stamens and carpels, which have been removed; *f*, withered stamens bent downwards; *g*, ovaries; *h*, stigmas which have placed themselves in the same spot that the dehiscent anthers occupied in the first stage; *i*, left half of the upper sepal, prolonged backwards into a long sheath for the spur (*i'*); *k*, left lateral sepal; *l*, left inferior sepal.

3 and 5, natural size; 1, 2, and 4, enlarged.

The five large, blue, expanded sepals make the flowers visible from far off to humble-bees, and serve the purpose of a corolla. The hollow spur of the uppermost sepal neither secretes nor contains honey. Its peculiar rough and crumpled wall serves rather as a cover for the organs which secrete and conceal the honey, which without it would be exposed to the rain; and also

it forces the humble-bees to suck the honey by the way that alone leads to fertilisation.

The two upper petals serve a very different purpose. In each the hollow pointed end of the spur ( $a^2$ , 3, 5), which is directed backwards and is inclosed in the hollow sepaline spur, secretes honey and becomes so full of it that part rises into the wide, half-conical<sup>1</sup> part of the spur which is open on the inner side ( $a'$ , 5). When both petals lie close to one another, they form together a hollow cone, which splits at the end into two points filled with honey, and guides the insect's proboscis, if long enough, safely to the honey, while by its length it prohibits the access of insects with shorter tongues. The anterior portions of the same petals produce the upper part of this hollow cone further forwards, and serve to give the bee's proboscis a convenient entrance and more certain path to the honey. Since these anterior portions of the upper petals separate easily on slight pressure from within, the whole head of a humble-bee may be thrust in between them, whereby the distance to the honey is shortened by 6 to 7 mm. The length of the hollow cone from its entrance to the anterior end of the honey-bearing prolongation is about 20 mm., and to the apex of the latter 26 to 28 mm.; so that, when the whole bee's head is thrust into the aperture, a proboscis 13 to 14 mm. long is needed to reach the honey, and one 19 to 22 mm. long to suck it all up. Hence, of all our native bees, *Anthophora pilipes*, F., and *Bombus hortorum*, L., can alone exhaust the honey.

The two lower petals are of service in several ways. Their anterior surfaces point by bundles of upright yellow hairs towards the entrance to the honey, that is to say, they serve as path-finders; and as they stand close together and bound this entrance below, they leave the bee no choice but to thrust its proboscis into the only proper place, viz., the interval between the two pairs of petals. Those parts of them immediately behind the entrance to the tube stand, on the other hand, so widely apart ( $b^*$ , 2) that they leave free space for the stamens and for the carpels (after the stamens have withered and bent back) to erect themselves in that part of the hollow cone lying close behind the entrance, where they inevitably come in contact with the under surface of the body and head of the bee.

With sufficient insect visits, which this handsome plant never fails to receive, cross-fertilisation is completely insured by the proterandrous dichogamy, and by the movements of stamens and carpels

<sup>1</sup> i.e. forming the longitudinal half section of a cone.

which are so completely in relation to the movements of the bee's head. The stamens in the unripe condition are bent down, when they dehisce they stand upright in the path of the bee's head, and when they are withered they sink completely down. The carpels erect themselves after the withering of the last of the stamens, and their stigmas then stand in the way of the bee's head. Self-fertilisation cannot take place in absence of insects. Of the two native bees whose proboscides are of sufficient length to suck the honey of this flower thoroughly, *Anthophora pilipes* has finished its period of flight and has disappeared when *D. elatum* flowers. *B. hortorum* therefore remains as the only indigenous bee fitted for sucking up the honey of *Delphinium*, and it is in fact found in great abundance on the flower. Many of our other species of bees are well fitted for sucking a portion of the honey, but I have never seen any of them, or any other species of insect, sucking on *D. elatum*. At Strassburg, *D. elatum* is visited also by *Anthophora personata*, Ill. ♀ (590, I.).

*Delphinium Staphysagria*, L., described and figured by Hildebrand (356, p. 473) agrees in most points of its floral arrangement with *D. elatum*, and is likewise fertilised by humble-bees.

15. *DELPHINIUM CONSOLIDA*, L., differs in the arrangement of its flower from *D. elatum* chiefly by the coalescence of the four petals into a single piece, which leads to the following modifications. The two upper petals unite by means of their backward directed processes into a single spur, the pointed end of which secretes and contains the honey; their expanded portions, which are turned forward, also coalesce lengthwise with one another, and therefore cannot be thrust apart on the entrance of the bee's head; but in conjunction with the lower petals they form a sheath which is well adapted to receive the bee's head, and is only open below. Here in the first stage of flowering it presents the anthers, and in the second the stigmas, for contact with the under surface of the bee's head. The lower petals, which thus form the side walls of the sheath or tube, unite with the upper ones, but not with one another, and yield laterally when the bee's head is thrust in. Path-finders and a lower boundary of the entrance to the spur are wanting here.

Since the cycle of development and movement of stamens and anthers agrees with that in *D. elatum*, cross-fertilisation is in like manner insured on the occurrence of insect-visits; and similarly, if they fail to occur, self-fertilisation is impossible.

In July, 1868, I assured myself of the actual certainty of cross-fertilisation by direct observation. I saw, in Thuringia, upon a field covered with wild larkspur in flower, numerous examples of *Bombus hortorum*, L. ♀ and ♂, sucking at the flowers of this species with such diligence that certainly no flower in its second period can have escaped being fertilised.

Since the length of the spur is about 15 mm. from its insertion, to which must be added the wide entrance, 7 mm. long, a proboscis fully 15 mm. long is needed to suck the honey in the normal way. Besides *Bombus hortorum*, L. (17 to 21), *B. agrorum*, F. (10 to 15), *B. fragrans*, K. (15) and *B. scabellus*, Sm. (14 to 15), some species of *Anthophora*, viz., *A. cæstivalis* Pz. (15), *A. retusa*, L. (16 to 17), and *A. pilipes*, F. (19 to 21), are all fitted for sucking the honey; but all must do so with greater loss of time, through having to force the head deep into the entrance to the spur, except *A. pilipes*, whose season is over when *Delphinium* comes into flower. *Bombus hortorum* seems thus to be the only species which is well adapted for the flower; but the diligence of this one species compensates the plant for the exclusion of all other insects. I have noticed *Satyrus* and species of *Hesperia* sucking at the flowers, and sinking their thin proboscides into the spur, but apparently they did not touch the anthers or stigmas.

Dr. Ogle gives in the *Popular Science Review* (631) a description of a species of larkspur which differs from those here described in that the honey secreted by the upper petals is contained in the spur of the posterior sepal. I unfortunately cannot determine which species of *Delphinium* is referred to as "the blue larkspur of our gardens."

*Delphinium Ajacis*, L., described by Sprengel, agrees in most points with *D. Consolida*, and is likewise fertilised by humble-bees.

16. *ACONITUM NAPELLUS*, L.—This plant is distributed throughout the Alps, especially about the Sennerei. It has distinctly proterandrous flowers, which are visited by humble-bees, as Sprengel long ago observed. The two posterior sepals cohere to form a helmet-shaped structure, which shelters the anthers and nectaries; the two lateral sepals give foothold to the mid and hindlegs of humble-bees; all four play, in addition, the part of petals, making the flower conspicuous by their blue colour. Of the four petals, the two anterior help to close in the essential organs laterally;

the two posterior are transformed into long-stalked nectaries, only accessible conveniently to humble-bees. The well-marked proterandry insures cross-fertilisation if humble-bees visit the flower, and, as a rule, prevents self-fertilisation in absence of insects (609).

17. *ACONITUM LYCOCTONUM*, L.—The structure of the flower is for the most part similar to that of *A. Napellus*, but the helmet and the nectaries are so exceedingly long that only an insect whose proboscis is very exceptionally long can reach the honey. In point of fact, in the plains (in a wood at Thüle, near Paderborn) I have found it visited exclusively by *Bombus hortorum*, L. ♀ (proboscis, 21 mm.), whose proboscis is the longest among lowland

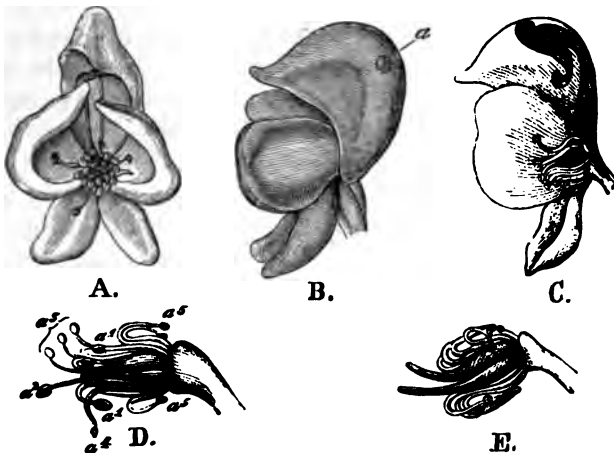


FIG. 29.—*Aconitum Napellus*, L.

- A.—Flower in first (male) stage. The anthers have become erect, have dehiscent, and are coated with white pollen.  
 B.—The same flower in side view. *a*, a hole bitten by *Bombus maurus*.  
 C.—Ditto, in longitudinal section.  
 D.—Essential organs in the first (male) stage. *a'*, anther bent backwards and not yet dehiscent; *a''*, ditto, becoming erect; *a'''*, ditto, erect, dehiscent, and covered with pollen; *a''''*, ditto, empty, and bending backwards; *a'''''*, ditto, empty, and bent quite backwards.  
 E.—Essential organs in the second (female) stage.  
 A—C, nat. size; D, E.  $\times 2$ .

humble-bees, and on the Alps exclusively by *B. opulentus*, Gerst. (22 mm.), whose proboscis is the longest among Alpine species. *B. opulentus* has not as yet been observed upon any other flower, either by Prof. Gerstäcker, who discovered and described it, or by myself (609).

*Aconitum septentrionale*, Koell., has likewise proterandrous flowers, figured by Axell (17).

*Pæonia Montan*, Sims., according to Delpino, is regularly fertilised by *Cetonix*, which lick the fleshy disk around the carpels.<sup>1</sup>

#### REVIEW OF THE RANUNCULACEÆ.

While the Umbelliferae form a numerous family where a certain sum of adaptations insuring cross-fertilisation has been inherited from ancestral forms and descends through all branches of the family, in *Ranunculaceæ*, on the other hand, we have a family whose separate divisions have developed for themselves quite distinct advantageous modifications. We see conspicuousness insured in *Ranunculus* by the petals; by the sepals in *Eranthis*, *Helleborus*, *Anemone*, *Caltha*; by both together in *Aquilegia* and *Delphinium*; by the stamens in *Thalictrum*. Honey is wanting in *Clematis*, *Thalictrum*, and *Anemone*: it is secreted by the sepals in certain *Pæonies*; by the petals in *Ranunculus*, *Eranthis*, *Helleborus*, *Nigella*, *Aquilegia*, *Delphinium*, *Aconitum*; by the filaments in *Atragene*; by the anthers in *Pulsatilla*; by the carpels in *Caltha*: it is sometimes easily accessible, at other times more or less deeply hidden. Such a variety of different adaptations is explained by supposing many different ways of attaining perfection to have been available for the plants when their flowers had not yet been modified so far as to insure cross-fertilisation.

An easily accessible situation of the honey in simple, regular flowers carried with it the advantage of abundant insect-visits; but at the same time the objection that the visitors crept about the flowers in various ways, often accomplishing only self-fertilisation, often leaving the flower still unfertilised. Honey more deeply placed brought the disadvantage that a great multitude of insects were shut out; but this advantage, that the bees with long proboscides had to move in a particular way to reach the honey, and so stamens and pistils could in a simple manner be arranged so as to render cross-fertilisation inevitable. We find self-fertilisation possible in all regular Ranunculaceous flowers with easily accessible honey; but prohibited by well-marked proterandry in all those with deeply situated honey, whether regular, as

<sup>1</sup> Lists of visitors to the following additional species are given in my *Weitere Beobachtungen*, pt. i.: *Clematis Vitalba*, L., *Thalictrum minus*, L., *Hepatica triloba*, Gil., *Pulsatilla vulgaris*, Mill., *Anemone silvestris*, L., *A. ranunculoides*, L., *Adonis vernalis*, L., *Myosurus minimus*, L., *Actæa spicata*, L.

*Aquilegia*, or irregular, as *Delphinium* and *Aconitum*; and so we may conclude that in the Ranunculaceæ the certainty of cross-fertilisation has been more effectually attained by flowers being specially adapted for a few species of bees, than by attracting a great multitude of different guests. We must however beware of taking this as a general conclusion; for in Umbelliferæ the still more open situation of the honey, aided by the massing together of many flowers, insures cross-fertilisation, through proterandrous dichogamy, even so far as to permit loss of the power of self-fertilisation.

Only those Ranunculaceæ seem to me to be adorned with blue colours which are cross-fertilised by bees, *e.g.* *Hepatica triloba*, which is fertilised by pollen-collecting bees, or the species of *Aquilegia*, *Aconitum*, and *Delphinium*, which seem adapted for humble-bees by the whole structure of their flowers. The easy transition in Hepaticas from blue to pink, and even to white, may be most easily explained as a case of reversion (*vide* also 609).

#### ORD. CALYCANTHACEÆ.

*Chimonanthus fragrans*, Lind., has, according to Hildebrand, proterogynous flowers. In the first stage, the still immature stamens are bent away from the stigmas, which receive pollen from other flowers; in the second stage, the ripe stamens arch over the stigmas and prevent access to them (356, p. 491). Delpino saw the flowers visited by an *Osmia* at Florence (177, p. 59).

*Calycanthus floridus*, L., according to Delpino, is markedly proterogynous with short-lived stigmas; it is devoid of honey, and is probably fertilised by *Cetonia* (177, p. 58).

#### ORD. MAGNOLIACEÆ.

*Illicium religiosum* has in the middle of the flower, according to Delpino, little papillæ, very rich in honey and resembling stigmatic papillæ, which probably serve as bait for a *Cetonia* (567).

*Magnolia Yulan*, Desf., is proterogynous. According to Delpino, bees fly into the upright flowers, and in the first period are neither able to creep up the smooth petals, nor to rise in flight from the short pistil which stands erect in the centre of the flower. They remain prisoners until in the second period the petals spread out, and the bees then fly away, dusted with pollen, to another flower (178, 360, p. 593).

*Magnolia grandiflora*, L.—Rose-beetles (*Cetonia aurata* and *stictica*) resort to the scarce opened flowers. They find shelter beneath the three inner petals, which form a vault over the stigmas, warmth which is so considerable that it is sensible to the touch, and honey lying on and between the stigmas. They remain in this pleasant refuge, until the sepals or petals fall off, and then, laden with pollen, they fly away to other flowers. In the first period only stigmas, and in the second only anthers, are mature, so self-fertilisation is impossible, and the beetles, flying from flower to flower, accomplish cross-fertilisation regularly (178, 360, p. 594).

ORD. ANONACEÆ.

*Asimina triloba*, Dunab., is proterogynous with short-lived stigmas. In the middle of the bell-shaped, pendulous flower rises a hemispherical mass of stamens, from the midst of which some stigmas protrude. The three inner petals, which secrete honey at their base, lie in the first period close upon the stamens; they compel the flies which visit the flower to touch the already mature stigmas on their way to the honey. Cross-fertilisation is effected if the flies come bringing pollen from an older flower. Delpino counted seven species of Diptera visiting the plant (178, p. 231; 360, p. 672).

ORD. BERBERIDEÆ.

18. *BERBERIS VULGARIS*, L.—Sprengel describes and figures the flowers as hanging down vertically. This, however, is seldom the case; most are horizontal or inclined obliquely downwards. They are not fully protected by their position from the weather, but the three inner sepals and the six petals, which as well as the sepals are curled inwards at their points, protect the stamens together with the honey-glands and honey from rain. The three inner sepals make the flower conspicuous by their yellow colour, and the petals completely embrace the stamens so long as the latter are undisturbed. The honey-glands are two thick, oval, fleshy, orange bodies, lying quite close together on the inner side and near the base of each petal. The filaments are so much expanded as to touch each other at the base; before being irritated they are bent so far back that each is in contact with the part of a petal below the honey-glands, and also with the adjacent halves of the two honey-glands. There is thus no room for the honey to mulate between petals and stamens, but it must flow into

the angles between stamens and ovary, which are always found to be quite full of honey. Every insect-visitor must thrust its proboscis into one of these angles; and in doing so it causes the two stamens which the base of its proboscis touches to spring inwards towards the pistil, and to dust with pollen one side of its head, which is thus shut in between two anthers and the stigma.

The stigma is represented by the papillose and viscid edge of a disc which surmounts the ovary and occupies the middle of the flower; one side of the insect's head, opposite to that touched by the stamen, comes in contact with the stigma. The insect usually flies away at once after the first drop of honey on being struck by the stamen, and as it thrusts its head or proboscis into the flower in many different ways as the different positions of the flower

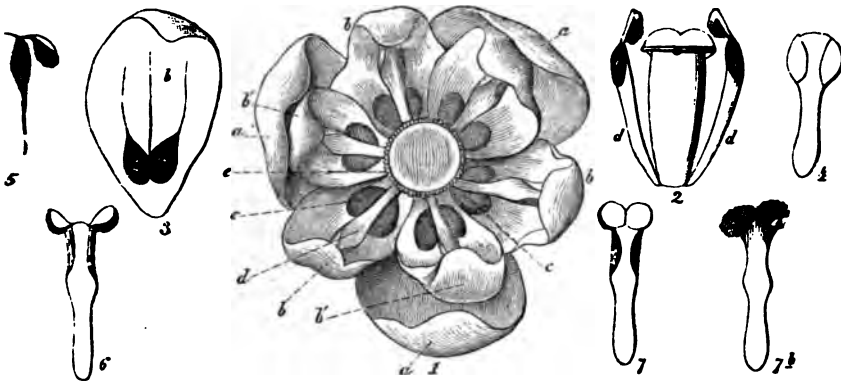


FIG. 30.—*Berberis vulgaris*, L.

- 1.—Flower seen from above. *a*, the three inner, larger sepals, which by their size and colour play the part of a corolla; *b*, outer, *b'*, inner petals; *c*, nectaries; *d*, filaments; *e*, stigma.
- 2.—Position of the stamens after springing inwards.
- 3.—Petal with its two thick fleshy, orange nectaries.
- 4–7.—Stamens in various stages of dehiscence, erection, and rotation of the anther-valves. 4, stamens with the anther-valves still closed: 5, the valve of the right anther-lobe has opened, and is beginning to move upwards, with the pollen attached to it; 6, both valves have nearly completed their movement of rotation, the pollen masses are directed towards the right and left; 7, both valves have turned in such a way that the pollen-masses face the centre of the flower, and touch one another with their adjacent edges; 7b, ditto, inner aspect.

require, now under now over the stigma, now to the right, now to the left, its head must soon be dusted all round with pollen, and it must fertilise every succeeding flower that it visits. It can only accomplish self-fertilisation if in the same flower it plunges its proboscis first to the right and then to the left, or first over and then under the stigma. In the case of the hive-bee I have distinctly observed that it seldom proceeds in this manner. It never makes a circuit of the flower, for it flies away and seeks

another as soon as it is struck by the stamens whose bases it has touched, and it rarely thrusts its proboscis a second time into the same flower. When it plants its forelegs upon the flower, it usually causes the greater number of the stamens to close in upon the pistil.

I have often seen humble-bees, on the other hand, thrust their proboscides again and again into the same flower.

It is clear from the above that Sprengel is in error when he explains the flower of the barberry as adapted for self-fertilisation; and this is proved most unequivocally by a closer examination of the movement of the anthers upon irritation.

Before the flower opens the anthers stand on a level with the stigma; they are closely applied to the stigma in the bud, but in the opening flower they are bent as far backwards as the surrounding petals allow. As soon as the petals begin to diverge, the anthers dehisce, the lid flying up and remaining attached only to the extreme end of the connective, which is here at its broadest. The anther-lid carries with it almost all the pollen, and after rising to its full height it turns that side which bears the pollen inwards towards the middle of the flower. If the stamens are now touched at their bases and made to move inwards, the masses of pollen do not come on a level with the stigma, but stand above it; so that even those parts of the masses of pollen which do not touch the insect, excluding some little scattered particles, do not come in contact with the stigma: the insect's head or proboscis, however, in being drawn back and rubbed against the masses of pollen gets dusted with pollen just in those parts which will come in contact with the stigma in other flowers.

If insect-visits altogether fail, then, as the flowers wither, the masses of pollen come of themselves into contact with the stigma through the bending inwards of the anthers. I have observed this in specimens kept in my room, but I cannot say what results follow self-fertilisation at such a late period.

Visitors: A. Diptera—(a) *Syrphidae*: (1) *Helophilus floreus*, L., very ab.; (2) *H. pendulus*, L.; (3) *Eristalis tenax*, L., ab.; (4) *E. arbustorum*, L.; (5) *E. nemorum*, L.; (6) *Rhingia rostrata*, L., ab.; (b) *Muscidae*: (7) *Onesia floralis*, R. D.; (8) *O. sepulcralis*, Mgn.; (9) *O. cognata*, Mgn.; (10) *Musca domestica*, L.; (11) *M. corvina*, F. B. Hymenoptera—(a) *Apidae*: (12) *Apis mellifica*, L. ♀, ab.; (13) *Bombus terrestris*, L. ♀; (14) *B. pratorum*, L. ♀; (15) *Andrena Trimmerana*, K. ♀; (16) *A. helvola*, L. ♂; (17) *A. fulvius*, K. ♂, ab.; (18) *A. fulva*, Schrk. ♀, moderately ab.; (19) *A. albicans*, K. ♀; (20) *A. Smithella*, K. ♀; (21) *Halictus rubicundus*, Chr. ♀.

(b) *Vespidæ*: (22) *Vespa holsatica*, F. ♀; (23) *V. rufa*, L. ♂. C. Coleoptera—(a) *Dermestidæ*: (24) *Attagenus pello*, L.; (b) *Coccinellidæ*: (25) *Coccinella 14punctata*, L. All were sucking honey; *Bombus pratorum* and *Andrena fulva* were also collecting pollen. See also 590, 1., and 609.

#### ORD. NYMPHÆACEÆ.

19. NUPHAR LUTEUM, Smith.—The sepals, as Sprengel clearly showed, have, by their increased size and the yellow colour of their upper surface, taken on the function of a corolla: the under side of the petals secretes honey. Sprengel found only small beetles of the genus *Meligethes* in the flowers: I have seen besides *Meligethes* various flies and other small beetles creeping about the flowers and flying from one to another; they effected self-fertilisation and cross-fertilisation indifferently. I was only able to catch *Oncisia floralis*, R.D. (*Muscidæ*), and *Donacia dentata*, Hoppe (*Chrysomelidæ*); both were richly dusted with pollen.

*Nymphaea alba*, L., and *Victoria regia*, Lind., are, in Delpino's opinion, fertilised by *Cetonia* and *Glaphyridæ*. See also No. 775.

#### ORD. PAPAVERACEÆ.

20. PAPAVER RHEAS, L.—The numerous anthers stand close round the stigma, and dehisce before the opening of the flower. They cover themselves with pollen, part of which reaches the lower part of the stigmatic lobes, while the higher central parts of the stigmatic lobes protrude free from pollen. Its flowers contain no honey, and are therefore visited solely by pollen-seeking insects, which find the broad stigmatic surface the most convenient place on which to alight. They necessarily accomplish cross-fertilisation if they have come from another flower, and this cross-fertilisation probably prevails in its action over the self-fertilisation which has already taken place.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Halictus sexnotatus*, K. ♀, very ab.; (2) *H. flavipes*, F. ♀, ab.; (3) *H. longulus*, Smith, ♀; (4) *H. cylindricus*, K. ♀; (5) *H. maculatus*, Sm. ♀; (6) *Andrena dorsata*, K. ♀, ab.; (7) *A. fulvicrus*, K. ♀; all collecting pollen, and dusted thickly with it. B. Diptera—*Syrphidæ*: (8) *Cheilosia*, f.p. C. Coleoptera—*Nitidulidæ*: (9) *Meligethes*, very ab., f.p. D. Orthoptera—(10) *Forficula auricularia*, L., both larvæ and perfect insects hiding in the base of the flower. See also No. 590, 1.

Whether, in default of insect-visits, the self-fertilisation which inevitably takes place leads to development has still to be decided by experiment. Probably it does so, as Hildebrand has found that

*Argemone ochroleuca*, *Glaucium luteum*, and *Papaver argemonoides* all bear seed when fertilised with their own pollen (358).

*Papaver Argemone*, L.—The flower has exactly the same structure as *P. Rhæas*, the only difference being that a smaller part of the stigmatic lobes is exposed to self-fertilisation.

In *Papaver dubium*, L., the stigma stands some millimeters above the level of the anthers, so that self-fertilisation can only take place in a down-turned position of the flower. Perhaps the fact that this species is much rarer than the others (in Westphalia, at least) is due to the impossibility of self-fertilisation.

*Papaver alpinum*, L., is homogamous, and (when cultivated) is sterile to its own pollen. The flowers are devoid of honey, and are visited by pollen-feeding Diptera (609).

*Papaver hybridum*, L., has cleistogamic flowers, at least when under cultivation (369).

21. *CHELIDONIUM MAJUS*, L.—In sunny weather the anthers dehisce laterally as the flower opens, and the stigma is developed at the same time. Since the stigma somewhat overtops the anthers, insects alighting in the middle of the flower touch the stigma first and accomplish cross-fertilisation, while those which alight on a petal and crawl inwards may accomplish either cross- or self-fertilisation. In dull weather the flowers remain closed longer, and the stamens dehisce within the as yet unopened flower, causing self-fertilisation.

The flowers contain no honey, and are visited and fertilised only by pollen-seeking insects.

Visitors : A. Hymenoptera—*Apidæ* : (1) *Bombus pratorum*, L. ♂ ; (2) *B. agrorum*, F. ♂ ; (3) *B. Rajellus*, Ill. ♀ —(all three alighted on the centre of the flower and swept pollen in great haste with the tarsal brushes of the fore and midlegs out of the anthers into the baskets on their hindlegs, and hardly spent two to three seconds on the flower before passing to another ; they effect cross-fertilisation regularly) ; (4) *Halictus cylindricus*, F. ♀ ; (5) *H. zonulus*, Sm. ♀ ; (6) *H. sexnotatus*, K. ♀ ; (7) *H. sexstrigatus*, Schenck, ♀ —(these small bees alight on the anthers and spend a much longer time on each flower, passing round upon the anthers. They only come in contact with the stigmas accidentally, and may effect self-fertilisation and cross-fertilisation indifferently). B. Diptera—(a) *Syrphidæ* : (8) *Syrphus balteatus*, Deg. ; (9) *S. ribesii*, L. ; (10) *Syrpita pipiens*, L. ; (11) *Ascia podagrica*, F. ; (12) *Rhingia rostrata*, L., all feeding on the pollen, and moving round the flower in the same way as the species of *Halictus* ; (b) *Empidæ* : (13) *Empis livida*, L. See also No. 590, I.

*Eschscholtzia Californica*, Chmss., furnishes an illustration of varying capacity for self-fertilisation. My brother Fritz Müller found

this species unfruitful in South Brazil, and Darwin found it fruitful in England, when fertilised with its own pollen. Plants which Fritz Müller raised in South Brazil from seed sent from England by Darwin yielded some seeds when fertilised with their own pollen, but far fewer than in England. Hildebrand found this species not absolutely barren, but very nearly so, when fertilised with its own pollen (358).

ORD. *FUMARIACEÆ*.

*Hypocoum procumbens*, L.—In the bud, the two inner petals receive all the pollen in two pockets developed upon their inner surface, and these pockets close up before the development of the stigma. On pressure from above, their edges separate and dust the object pressing them with pollen. The stigmatic papillæ do not attain their full development until some time after the opening of the flower, and after the pistil has grown up above the level of the pollen-sacs, so that in each flower insects come in contact first with the stigma and then with the pollen. Cross-fertilisation is insured (in case of insect-visits) first by proterandry, and secondly by the projecting situation of the stigma (358).

*Hypocoum grandiflorum*.—Hildebrand found that the flowers of this species were very nearly though not absolutely barren when fertilised with their own pollen or with pollen from another flower of the same plant (358).

22. *DICLYTRA SPECTABILIS*, D.C.—The heart-shaped pendulous flowers contain honey in the two pouches at the base of the outer semi-cordate petals. Each of these two petals incloses three stamens which follow the contour of its wall and then together form a channel leading from the middle of the flower to the honey. The exerted ends of the six stamens project straight downwards, lying close together around the pistil, and being themselves surrounded by the hood-like ends of the two inner petals, which cohere at the points.

Between the hood-shaped end of the inner petal and the curled end of the outer one, there remains on the right and left a canal leading to the honey. If a bee hanging from the flower thrusts its proboscis into one of the two canals, the lower surface of its abdomen presses both the hood and the flexible stamens towards the opposite side; and the stigma, which is at the end of a stiff style and therefore escapes being pushed aside, is rubbed by the

hairs on the lower surface of the bee's body. When the bee flies away the hood returns to its former position and again incloses the stamens and pistil. At each visit this action is performed twice, once on the right and once on the left, since there are two honey-sacs and two canals leading to them. Thus in young flowers the pollen adhering to the stigma is brushed off on to the hairy body of the bee, and in older flowers, which have been already robbed of their own pollen, pollen from other flowers is brought and applied to the stigma. Hildebrand saw humble-bees acting in the manner described. Since the proboscides of our humble-bees vary from 7 to 21 mm., and the canals leading to the honey in *Diclytra* are 18 to 20 mm. long, the action of the different visitors deserves closer examination.

I have only seen *Bombus hortorum*, L. ♀ (20 to 21), and *Anthophora pilipes*, F. ♀ (19 to 20), both in fair abundance, sucking this flower in the normal way: they sucked each flower twice, once on each side. *Bombus terrestris*, L. ♀, whose proboscis is only 7 to 9 mm. long, climbs on to the upper part of the flower and bites a hole into one of the honey-sacs; it tries to introduce its proboscis through the hole it has made, and if it does not at once succeed, it bites several times, and at last succeeds in stealing the honey out of both the pouches.<sup>1</sup> I have seen *Bombus pratorum*, L. ♀ (11 to 12), and *B. Rajellus*, Ill. (12 to 13), act in the same way. *Osmia rufa*, L. ♀ (9), *Megachile centuncularis*, L. ♂ (6 to 7), and *Apis mellifica*, L. ♀ (6), often make use of the holes which humble-bees have bitten, and which few flowers are free from.

The action of the hive-bee on flowers of *Diclytra* convinced me of the advantage that flowers derive from having convenient landing-places for insects. If the bee tried to steal honey by means of holes made by *Bombus terrestris*, it found no such resting-place, but catching hold of the edge with some of its legs, it groped about with the others on the smooth surface, and so stood insecure and wasted much time.

*Diclytra eximia*, D.C.—The flower has been thoroughly described and figured by Hildebrand (358). It resembles *D. spectabilis*, but the space for the lateral bending of the hood is smaller and the passage to the honey shorter.

In *Diclytra cucullaria*, D.C., the outer petals are provided with long spurs and the honey is secreted by two long processes of the middle stamens lodged in these spurs (358).

<sup>1</sup> In North America, *Diclytra Canadensis* is bitten in the same way by the short-lipped bee *Bombus Virginicus*, Oliv. (736).

23. *CORYDALIS CAVA*, Schweigg. and Kört. The flower is figured and described by Hildebrand (351, 358).

In contrast to the pendulous flowers of *Diclytra* and *Adlumia*, which are symmetrical about two planes perpendicular to one another, and permit a double motion of the hood, to right and left, we have in *Corydalis cava* horizontal flowers symmetrical about one perpendicular plane, and whose hood can only be thrust by insects in one direction, viz. downwards. The two outer petals, which are here superior and inferior, have ceased to be symmetrical, the upper one being produced into a long spur, curved downwards at the end, and reaching some 12 mm. backwards over the flower-stalk. In this spur is lodged a common prolongation of the upper stamens, which secretes honey and extends as far as the curved part of the spur.

The two inner petals stand at the sides, and are fused with the upper petal at their bases; they are symmetrical, and unite at the apex to form a hood. A bee, to reach the honey stored at the end of the spur, must stand on the lower petal or on the hood, and thrust its proboscis between the hood and the upper petal; in doing this, it presses down the hood, and rubs the under surface of its head on the stigma, which, being placed on a stiff pistil, does not bend downwards, and has been covered with pollen before the opening of the flower. The hood, on withdrawal of the pressure, springs back into its former place, and covers the pistil and stamens as before.

So, in young flowers, bees dust the lower part of their heads with pollen; in older ones they supply the stigma with pollen from previously visited flowers. As the bees habitually go from below upwards on each plant, they bring pollen to the lower and older flowers of one plant from the upper and younger flowers of another, and thus regularly induce crossing of separate stocks. This is very noteworthy, since Hildebrand has shown by many experiments that the flowers of *C. cava* are absolutely barren to their own pollen, very slightly fertile to pollen from another flower of the same plant, and only thoroughly fertile when impregnated with pollen from a different plant.

Since the spur of *C. cava* is 12 mm. long, and is at the very most filled with honey to the extent of 4 or 5 mm., it is quite impossible for the hive-bee with its proboscis of 6 mm. to reach the honey in the legitimate way. *Bombus terrestris*, L. ♀, might succeed better with its proboscis of 7 to 9 mm., occasionally even 10 mm.; but even this species soon gives up thrusting its proboscis

must touch simultaneously the stigma and the pollen-covered faces of three anthers, one short and two long. If, in continued bad weather, the flowers do not open fully, self-fertilisation is effected by the longer anthers, as in *N. silvestre* (590, I., 609).

28. ARMORACIA AMPHIBIA, Koch. (*Nasturtium amphibium*, R. Br.).—The structure of the flower resembles that of *Nasturtium silvestre*.

Visitors : A. Hymenoptera—*Tenthredinidæ* : (1) *Tenthredo notha*, Kl., very abundant, passing from flower to flower and dipping its proboscis down to suck,—head and thorax richly dusted with pollen. B. Diptera—(a) *Empidæ* : (2) *Empis livida*, L., s. ; (b) *Syrphidæ* : (3) *Rhingia rostrata*, L., s. ; (4) *Syritta pipiens*, L., s. ; (5) *Eristalis arbustorum*, L., s.

*Arabis alpina*, L., is homogamous (609).

*Arabis bellidifolia*, Jacq., is proterogynous, with long-lived stigmas (609).

29. ARABIS HIRSUTA, R. Br.—The arrangement of the flowers differs from that of *Nasturtium silvestre* in that only two glands lying internal to the base of the shorter stamens secrete honey, and that in most flowers the longer stamens arch over the stigma, and shed their pollen on it, if it is not removed by insect visitors. Flowers also occur in which the anthers of the longer stamens stand on the same level as the stigma, and shed their pollen in immediate contact with it.

Visitors : A. Hymenoptera—(a) *Sphegidæ* : (1) *Ammophila sabulosa*, L., s. ; (b) *Apidæ* : (2) *Apis mellifica*, L. ♀, s. ; (3) *Halictus sexnotatus*, K. ♀, c.p. ; (4) *Andrena albicrus*, K. ♂, s. B. Lepidoptera—*Bombyces* : (5) *Euprepia Jacobææ*, L., s. C. Diptera—*Syrphidæ* : *Syritta pipiens*, L., s.

30. CARDAMINE PRATENSIS, L.—This species differs greatly from the preceding forms in the situation of its honey, in the position of its anthers, in the conspicuousness of its flowers, and hence also in the number of its visitors. Two large honey-glands surround the bases of the two shorter stamens as green fleshy cushions which are most marked at the outside and secrete their honey at that point : two smaller honey-glands occupy the position of the two aborted smaller stamens,<sup>1</sup> i.e. they are placed antero-posteriorly, between the

<sup>1</sup> Eichler's view of the floral symmetry and number of the parts in Cruciferae is different from that advanced here by the author, and is now more generally adopted. He regards the number two as the basis of the floral whorls, and looks upon the four petals and the four inner stamens as due to the chorisis respectively of two antero-posterior petals and stamens. On this view the whorls alternate regularly with each other, and the flower is symmetrical. (Eichler, *Blüthendiagramme*, vol. ii.)

pairs of long stamens. The honey secreted by these four glands accumulates in the pouched bases of the sepals. Since the calyx in this case serves to hold the honey it is more persistent than in most other Crucifers, and the sepals are unusually large, in relation to the great size of the honey-glands; those which receive the honey from the larger glands are broader and more swollen at the base than the two others, so that one may tell by looking at the calyx from below where in the flowers the shorter stamens are placed. On tearing off the sepals, a honey-gland is seen between the claws of each pair of adjacent petals.

In the young bud all the six anthers are turned towards the pistil, which projects above them. Before the flower opens, the



FIG. 32.—*Cardamine pratensis*, L.

- 1.—Flower, from above.
- 2.—Ditto, in side view, after removal of the two anterior petals.
- 3.—Essential organs and nectaries (n), enlarged.

four inner stamens elongate and overtop the stigma, and make a quarter of a revolution outwards, each one towards the small stamen nearest to it: so that now an insect, in trying to reach the honey of one of the larger glands, must rub its head or proboscis against the pollen-bearing surface of one of the taller anthers.

In cold, rainy weather flowers are often found in which the revolution is incomplete, or does not take place at all, and in such cases the pollen of the longer stamens falls of itself upon the stigma. The shorter stamens always remain with the side at which they dehisce turned inwards towards the stigma, so that the pollen is rubbed off by the head or proboscis of any insect which is

making for the smaller honey-glands. With reference to the likelihood of cross-fertilisation the same remarks hold good as in the case of *Nasturtium silvestre*. In many flowers the shorter anthers stand lower than the stigma, in others on a level with it or even higher. In the two last cases they may aid in self-fertilisation.

*Cardamine pratensis* surpasses all the other Crucifers which grow wild near Lippstadt in the conspicuousness of its flowers and the abundance of its honey, and consequently in the number of its insect visitors.

A. Hymenoptera—*Apidae*: (1) *Halictus cylindricus*, F. ♀, c.p.; (2) *Andrena dorsata*, K. ♀, s.; (3) *A. parvula*, K. ♀ ♂, c.p. and s.; (4) *A. Gwynana*, K. ♀, c.p., (once it flew straight from the *Cardamine* to a short-styled flower of *Primula elatior* and gathered pollen there also); (5) *Nomada lateralis*, Pz. ♀, s.; (6) *N. lineola*, Pz. ♂, s.; (7) *Osmia rufa*, L. ♂, s.; (8) *Bombus terrestris*, L. ♀, s.; (9) *Apis mellifica*, L. ♀, very ab., c.p. and s. B. Diptera—(a) *Bombylidae*: (10) *Bombylius major*, L., once, hovering over the flower and sucking,—it passed straight from the *Cardamine* to *Primula elatior*; (11) *B. discolor*, Mgn., s.; (b) *Empidæ*: (12) *Empis opaca*, F., s.; (c) *Syrphidæ*: (13) *Rhingia rostrata*, L., f.p.; (14) *Helophilus pendulus*, L., s.; (d) *Muscidæ*: (15) *Anthomyia* sp., f.p. C. Lepidoptera—(16) *Rhodocera rhamni*, L.; (17) *Pieris brassicæ*, L.; (18) *P. napi*, L.; (19) *Anthocharis cardamines*, L. D. Coleoptera—(a) *Nitidulidæ*: (20) *Meligethes*, ab., l.h.; (b) *Staphylinidæ*: (21) *Omalium florale*, Pk., very ab. E. Thysanoptera—(22) *Thrips*, s. and f.p. See also 590, 1.

*Cardamine chenopodifolia*, Pers., has cleistogamic flowers which burrow into the earth (296).

*Cardamine impatiens*, L., is visited by *Andrena albicans*, K. ♀ (590, 1.).

*Barbarea vulgaris*, R. Br.—Each of the two shorter stamens has on either side of its base a small, green, fleshy honey-gland; a somewhat larger honey-gland is placed between each pair of longer stamens, externally to their bases, in the position of the two short stamens that have disappeared. On each of the six glands a colourless drop of fluid may be seen in fine weather. The anthers are placed as if the glands between the longer stamens were absent. The taller stamens, which overtop the stigma, make a quarter of a revolution towards the neighbouring short stamens; this movement begins with the dehiscence of the anthers immediately after the flower expands, and is just finished when the anther is completely covered on one side with pollen. The two shorter anthers, which are on a level with the stigma, remain turned towards it even after dehiscence, so that the position of the anthers is the same as in

*Nasturtium officinale*, though the number of glands is as in *N. silvestre* (590, I.).

31. *DRABA Verna*, L.—Four small, green, fleshy honey-glands occur in each flower, each being situated between the bases of a short stamen and the long one next it; so that the base of each short stamen stands between two honey-glands. Anthers and stigma ripen together. The longer stamens reach to a level with the stigma, and stand close around it: they dehisce on those sides which are turned towards the stigma, and always dust it with pollen; the shorter stamens also turn their pollen-covered surfaces towards the stigma, but stand below it. Honey-seeking insects must thrust their proboscides between the stigma and one of the shorter stamens into the base of the flower, and so dust themselves with pollen, especially from the shorter stamens, and carry it elsewhere. Cross-fertilisation is chiefly effected with pollen from the shorter stamens, while the four longer ones regularly effect self-fertilisation. Hildebrand has found by experiment that the latter is productive. We may understand the extensive use that this plant makes of self-fertilisation if we consider how small and inconspicuous the flowers are, how small a supply of pollen or honey they can yield, and how few insects they are for these reasons visited by. I have only observed three species of bees on *Draba verna*, viz:—

(1) *Apis mellifica*, L. ♀, c.p. (April 10, 1868); (2) *Andrena parvula*, K. ♀, s. (March 28, 1869); (3) *Halictus* sp. ♀, s. (March 28, 1869).

*Draba aizoides*, L., is proterogynous with persistent stigmas (609).

*Draba Wahlenbergii*, Hartm., is homogamous (609).

32. *COCHLEARIA OFFICINALIS*, L.—Near Niederalma, I saw the following insects on flowers of this plant (July 12, 1869):—

A. Diptera—*Syrphidæ*: (1) *Eristalis tenax*, L.; (2) *Helophilus florens*, L.; (3) *Melanostoma mellina*, L., ab., all three both s. and c.p. B. Coleoptera—(4) *Cetonia aurata*, L., gnawing the parts of the flower.

*Kerneria saxatilis*, Rich., is homogamous. The four longer stamens bend laterally almost to a right angle, so that their anthers come to lie quite close to those of the shorter stamens (609).

*Thlaspi arvense*, L., is homogamous. The shorter stamens are concerned in cross-fertilisation; the longer, in case of need, effect self-fertilisation (590, II.).

*Pringlea antiscorbutica*, Hook., grows on the tempestuous shores of Kerguelen's Island, where winged insects cannot exist, because at every flight they run the risk of being drowned. Under these circumstances the plant has become modified for fertilisation by the wind, acquiring exserted anthers and long filiform stigmatic papillæ. It still retains traces of its descent from entomophilous ancestors; for while on the great part of the island it is devoid of petals, it occurs abundantly in sheltered places with petals. On the same raceme some flowers may possess only a single petal, others two, three, or four; and the petals, though usually of a pale greenish colour, are occasionally adorned with purple (216, 372).



FIG. 53.—*Kerneria saxatilis*, Rich.

A.—Flower, viewed from above.

B.—Ditto, from the side, after removal of two petals ( $\times 7$ ). *k*, short stamens.

33. *TEESDALIA NUDICAULIS*, R. Br.—The structure of this flower, whose longest petals are only two mm. long, differs remarkably from our other native Crucifers.

During the period of flowering, the flowers are aggregated into a flat surface, whose outermost petals are larger than the others, as in the case of Umbellifers. But in *Teesdalia*, as flowering progresses, the axis lengthens and draws out the flat surface into a raceme, so that each flower comes to stand at the edge in its turn. So it is not only certain flowers that stand from the beginning at the edge, which have the corolla specially developed on the outer side (as in many *Umbelliferae* and *Compositae*), and thus become symmetrical about a single axis (zygomorphic); but all the flowers have their outer petals specially developed, and thus acquire a zygomorphic symmetry.

Each flower has a superior (*s*), an inferior (*s'*), and two lateral sepals (*s<sup>2</sup>*), which help to render the flower conspicuous by white tips and a white median ridge; but conspicuousness is chiefly

attained through the white colour of the petals, of which the flower has two superolateral ones ( $p$ ), and two anterolateral ( $p'$ ), twice or three times as long as the former. In addition, there are petal-like appendages ( $y$ , 4,  $x$ , 2, 3) to the two lateral and shorter stamens ( $a$ ), and others, still larger, to the four longer ones ( $a'$ ,  $a^2$ ). The petal-like appendages of these four inner stamens closely surround the ovary, which is flattened antero-posteriorly, sharp-edged on each side, bent slightly forwards, and divided symmetrically by a partition wall.

The centre of the base of each petal has a small pouch, and just above this each staminal protuberance is provided with a similar structure; between the two lies a little drop of honey, and concealed beneath this is a small, greenish, fleshy honey-gland. Both the petals and the longer stamens can be torn away without injuring or removing the glands; which seem therefore to belong to the base of the flower (receptacle).



FIG. 34.—*Teesdalia nudicaulis*, R. Br.

- 1.—Flower, from above.
  - 2.—Anterior half of flower.
  - 3.—One of the longer stamens, with a nectary, seen from without.
  - 4.—One of the two shorter stamens, from without.
- $x$ ,  $y$ , foliar appendages of filaments;  $n$ , nectary.

Before the flower opens, the six anthers are all turned towards the stigma, the four longer ones overtopping it slightly, the others standing on a level with it. After the flower has expanded, all six stamens twist through a quarter of a revolution; each of the longer ones turns its anther towards the adjacent shorter one; while each of the two shorter ones turns towards the outside of the flower. Now the anthers dehisce, and at the same time the stigma becomes mature. Insects in reaching the two outer honey-drops cannot avoid touching with their head or proboscis the pollen-covered sides of the two neighbouring anthers; while those that suck the inner drops only come in contact with the pollen of a single anther. Owing to the small size of the flower, the insect must touch the stigma at the same time with another

part of its proboscis or head. As we have seen in other cases, this must regularly lead to cross-fertilisation if the insect thrusts its head only once into the flower, but may equally well produce self-fertilisation if it does so more than once. In absence of insects self-fertilisation is always accomplished by means of the longer stamens.

On April 27 and 28, 1872, I and my son Hermann saw the following insects visit a luxuriant patch of *Teesdalia* in sunny weather:—

A. Hymenoptera—*Apidae*: (1) *Sphecodes ephippia*, L., sucking on thirteen inflorescences successively. B. Coleoptera—(a) *Chrysomelidae*: (2) *Haltica nemorum*, L., three specimens, apparently sucking; (3) *Plectroscelis dentipes*, E. H., one specimen, do.; (4) *Cassida nebulosa*, L., two specimens flew on to the inflorescence without making use of the flowers; (b) *Curculionidae*: (5) *Ceutorhynchus pumilio*, Gylh., two specimens, s.; (c) *Elateridae*: (6) *Limonius parvulus*, Pz.; (d) *Hydrophilidae*: (7) *Cereyon anale*, Pk. (these last two beetles also settled on the flowers, but I could not see that they made use of them in any way). C. Diptera—(a) *Syrphidae*: (8) *Melithreptus* sp.; (9) *Ascia podagrica*, F., both f.p.; (b) *Muscidae*: (10) *Sepsis putris*, L., ab., s. Also many minute Muscidae and gnats, 1 to 4 mm. long.

*Biscutella lavigata*, L., is homogamous. I have found it visited by thirty-six species of insects, mostly Diptera (609).

*Hesperis tristis*, L.—This plant, by elongation and close approximation of the sepals and the claws of the petals, excludes all insects except Lepidoptera from its honey. By the time of expanding and emitting its perfume it has become adapted for cross-fertilisation by crepuscular and nocturnal forms (570, vol. xii.).

34. *HESPERIS MATRONALIS*, L.—Honey is secreted by two very large, green, fleshy glands surrounding the base of the shorter stamens, and especially developed on their inner sides; it collects on each side of the flower between the pistil and the bases of the three stamens of that side.

The taller anthers stand at the entrance of the flower, and only project beyond it when they have withered. The shorter stand a little deeper within the flower, and when they dehisce their tips closely surround the stigma, which is afterwards protruded beyond the flower by the lengthening of the pistil. All the anthers dehisce inwards, and cover the stigma with pollen. If insect-visits take place at the proper time, cross-fertilisation is also effected: regularly by the honey-seeking species, for they touch

stigma and stamens with opposite sides of the proboscis, and, at least sometimes, by pollen-seeking forms.

Visitors : A. Diptera—(a) *Stratiomyidæ* : (1) *Nemotelus pantherinus*, L. f.p. ; (b) *Syrphidæ* : (2) *Chrysogaster ænea*, Mgn. (Tekl. B.), f.p. ; (3) *Eristalis nemorum*, L. ; (4) *E. tenax*, L., both f.p. ; (5) *Volucella pellucens*, L. (Tekl. B.) ; (6) *Rhingia rostrata*, s., very ab. B. Hymenoptera—*Apidæ* : (7) *Halictus leucopus*, K. ♀ ; (8) *Andrena albicans*, K. ♀ ; (9) *Apis mellifica*, L. ♀, all three c.p. C. Lepidoptera—(10) *Pieris brassicæ*, L., s. ; (11) *P. napi*, L., s. ; (12) *P. rapæ*, L., s. D. Coleoptera—(13) *Anthocomus fasciatus*, L. See also, 590, 11.

35. *ALLIARIA OFFICINALIS*, Andrzej. (*Sisymbrium Alliaria*, Scop).—The honey-glands agree in character and situation with those of *Cardamine pratensis*. But while in *C. pratensis* the honey is secreted towards the outside, and collects in the pouched sepals, in *A. officinalis* it exudes inwards from the glands at the base of the short stamens, and forms four drops in the base of the flower. These each lie between a short stamen and the adjacent long one, and finally fill the lower part of the space between the stamens and pistil, to which parts they adhere firmly. I have never observed secretion on the part of those glands which occupy the position of the two aborted short stamens ; they seem to be functionless ancestral structures. The sepals, which persist as receptacles for the honey in *C. pratensis*, are in *A. officinalis* only useful in the bud, as a protection for the parts within, and by contributing by their white colour to the conspicuousness of the inflorescence ; when the flower expands they cease to be of use and easily drop off.

All the anthers dehisce inwards ; the inner ones surround the stigma so closely that they always effect self-fertilisation, and this, as I have proved, leads to the production of good seed. Cross-fertilisation must, as in the foregoing species, be effected very frequently by honey-seeking insects, and at times by pollen-seeking species ; and it probably then outstrips self-fertilisation in its action.

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. B. Diptera—(a) *Syrphidæ* : (2) *Syrphus decorus*, Mgn. (Tekl. B.) ; (3) *Rhingia rostrata*, L., s. ; (b) *Muscidæ* : (4) *Anthomyia*, s. C. Coleoptera—(a) *Nitidulidæ* : (5) *Meligethes*, ab. ; (6) *Epuræa* ; (b) *Curculionidæ* : (7) *Ceutorhynchus*, a minute species. See also 590, 11.

36. *SISYMBRIUM OFFICINALE*, Scop.—The structure of the flower agrees fairly with that of the foregoing species. Each of

the two shorter stamens has on either side of its base a honey-gland; each of the four honey-drops secreted by these lies in the space bounded by one of the shorter stamens, the adjacent long one, and the pistil. The anthers ripen along with the stigma, which their pollen-covered sides face; the taller anthers overtop the stigma and arch inwards, the shorter stand on a level with it, and curve slightly outwards. In default of insect-visits pollen regularly falls upon the stigma from the four long stamens.

The flowers are very small, and for that reason insect-visits are scarce. The honey, however, seems to be particularly liked by certain insects. On June 27, 1868, on a waste patch where *S. officinale* and *Capsella bursa-pastoris* were growing abundantly with several other plants, I noticed *Pieris napi*, L., and *P. rapæ*, L., flying about in great numbers, and sucking the flowers of this plant only. The point of the insect's proboscis is thrust in between the stigma and the anthers. I also saw several specimens of *Andrena dorsata*, K. ♀, in quest of pollen: they were probably as likely or more likely to effect self-fertilisation than cross-fertilisation.

Visitors: A. Hymenoptera—*Apidae*: (1) *Andrena dorsata*, K., c.p. and f.p. B. Lepidoptera—*Rhopalocera*: (2) *Pieris napi*, L., s.; (3) *P. rapæ* L., s. See also 590, II.

37. *CAPSELLA BURSA-PASTORIS*, D.C.—The only difference to be noted between this and the foregoing is that the long stamens stand on a level with the stigma, and effect self-fertilisation regularly. Specimens which I kept in a room and protected from insects were fully productive.

Visitors: Diptera—(a) *Syrphidae*: (1) *Eristalis nemorum*, L., s. and f.p.; (2) *Syrphus balteatus*, Deg., do.; (3) *Syrphia pipiens*, L.; (4) *Ascia podagrica* F., s.; (5) *Melithreptus scriptus*, L.; (6) *M. taniatus*, Mgn.; (7) *M. pictus*, Mgn., the last three s. and f.p.; (b) *Muscidae*: (8) *Anthomyia*, s. See also 590, II.

38. *LEPIDIUM SATIVUM*, L.—The flowers are inconspicuous, but their strong scent is perceptible even to us several paces off. Owing doubtless to this, they are more abundantly visited than any other Crucifer which I have observed, partly for their honey, partly for their pollen. The honey is secreted by four green, fleshy glands, situated between the long and short stamens, and opposite to the petals; the two long stamens on each side face the broad surface of the silicula, and arise close together between the two lateral petals. The anthers dehisce introrsely, and the

stamens undergo no twisting, but in sunny weather they bend backwards as far as the nearly upright sepals permit them. As to the likelihood of cross- or self-fertilisation, the same holds as in the case of *Nasturtium silvestre*. When in rainy weather the flowers do not fully open, or when they close up again without being visited by insects, self-fertilisation occurs.

Visitors : A. Diptera—(a) *Bombylidæ* : (1) *Argyromœba sinuata*, Fallen ; (b) *Syrphidæ* : (2) *Eristalis arbustorum*, L. ; (3) *E. nemorum*, L. ; (4) *E. sepulcralis*, L. ; (5) *Helophilus florens*, L. ; (6) *Syritta pipiens*, L., very ab. ; (7) *Melithreptus tæniatus*, Mgn. ; (8) *Ascia podagrica*, F., very ab. ; (9) *Pipiza chalybeata*, Mgn., all these *Syrphidæ* now s., now f.p. ; (c) *Muscidæ* : (10) *Siphona cristata*, F. B. Hymenoptera—(a) *Ichneumonidæ* : stragglers ; (b) *Sphegidæ* : (11) *Oxybelus bellus*, Dlb., ab. ; (12) *O. uniglumis*, L., very ab. ; (13) *Cemonus unicolor*, F. ; (14) *Cerceris variabilis*, Schrk., very ab. ; (c) *Chrysidæ* : (15) *Hedychrum lucidulum*, F. ♂ ; (d) *Apidæ* : (16) *Prosopis communis*, Nyl. ♂ ♀, very ab., s. and f.p. ; (17) *P. armillata*, Nyl. ♂ ♀, do. ; (18) *Halictus nitidiusculus*, K. ♀, s. ; (19) *H. lucidulus*, Schck. ♀, s. ; (20) *Andrena parvula*, K. ♀ ; (21) *A. pilipes*, F. ♂, s. C. Coleoptera—(a) *Dermestidæ* : (22) *Anthrenus pimpinellæ*, F. ; (b) *Malacodermata* : (23) *Dasytes flavipes*, F. ; (24) *Anthocomus fasciatus*, F. ; (25) *Malachius bipustulatus*, F., gnawing the anthers and petals. D. Lepidoptera—(26) *Sesia tipuliformis*, L., s., frequent.

*Hutchinsia alpina*, R. Br., is proterogynous with persistent stigma. It is visited and cross-fertilised by Diptera (609).

39. BRASSICA OLERACEA, L.—Two honey-glands lie on the inner side of the bases of the two short stamens, and two others occupy the position of the aborted pair, *i.e.* are antero-posterior. The honey-drops secreted by the two former distribute themselves each between a short stamen, the two adjacent long ones, and the pistil, and are easily visible on looking straight downwards into an open flower ; the drops from the other pair of glands lie outside between the two adjacent long stamens, and these drops increase until they sometimes reach the sepals. The two shorter anthers stand sometimes on a level with the stigma, usually however they are not so high ; they curve outwards, but their pollen-covered sides face the centre of the flower. The long stamens perform a quarter- or half-revolution without increasing their distance from the centre of the flower, so that the pollen-covered sides of their anthers are either turned towards the neighbouring short stamen, or else directly outwards. An insect in sucking the honey at the base of a short stamen touches with one side of its head or proboscis the stigma, and with the other a short stamen and usually a long one at the same time: the

other two drops of honey can be reached without touching the stigma, and seem to afford no aid in fertilisation. In default of insect-visits the upper part of each of the long anthers bends back so far as to touch the stigma, thus effecting self-fertilisation.

This self-fertilisation is probably efficient: at least *B. rapa*, L., was found by Hildebrand to produce seed when self-fertilised (351). In sunny weather I have always found the honey very evident. Sachs,<sup>1</sup> who says "the dark-green nectaries lying between the stamens of *Brassica* retain their secretion within them," has probably examined the flowers in dull weather.

Visitors: A. Coleoptera—*Nitidulidæ*: (1) *Meligethes*, very ab., feeding on the petals and on pollen. B. Hymenoptera—*Apidæ*: (2) *Andrena nigroaenea*, K. ♀, s.; (3) *A. Gwynana*, K. ♀, s. and f.p.; (4) *A. fulvicrus*, K. ♀, c.p.; (5) *A. nana*, K. ♀, s. and f.p.; (6) *Halictus cylindricus*, K. ♀; (7) *Apis mellifica*, L. ♂, s. and f.p. (I did not see the hive-bee preserve any definite order in visiting flowers of this plant; frequently a bee after visiting a second flower returned to the first). C. Thysanoptera—(8) *Thrips*, ab.

40. *SINAPIS ARVENSIS*, L.—The honey-glands are placed as in *Brassica*. When the calyx expands, the glands are visible and accessible from the outside, and insects can reach them without touching the essential organs of the flower. The close aggregation of the flowers however renders it more convenient for the insect to thrust its proboscis down between the stamens, and in point of fact I have never seen an insect visitor obtain the honey from the outside. The twisting of the stamens and the likelihood of cross-fertilisation are as in *Cardamine pratensis*; as the flowers wither, however, the anthers turn their pollen-covered sides upwards, and finally their tips bend downwards, so that they effect self-fertilisation if their pollen has not already been removed.

Visitors: A. Diptera—*Syrphidæ*: (1) *Eristalis æneus*, Pz.; (2) *E. arbutorum*, L.; (3) *Rhingia rostrata*, L., all these both s. and f.p. B. Hymenoptera—(a) *Tenthredinidæ*: (4) *Cephus spinipes*, Pz., and several small sp. in great abundance, l.h. and f.p.; (b) *Apidæ*: (5) *Halictus leucozonius*, Schrk. ♀, c.p.; (6) *Andrena nana*, K. ♂, s.; (7) *Apis mellifica*, L. ♂, very ab., both s. and c.p. (I found it collecting pollen on *Sinapis* on Oct. 2, 1869). C. Coleoptera—(8) *Coccinella 7punctata*, L., l.h. D. Lepidoptera—(9) *Euclidia glyphica*, L., s. See also 590, II.

A variety of *Sinapis arvensis* bears cleistogamic flowers at St. Croix, where the temperature is 25° C. (762).

<sup>1</sup> *Lehrbuch der Botanik*, 2nd ed., p. 110.

41. *RAPHANUS RAPHANISTRUM*, L., has four honey-glands arranged as in *S. arvensis*, but all the anthers remain turned towards the stigma, the shorter ones standing on a level with it, so that the chance of self-fertilisation is increased.

I have seen the honey-bee, which usually confines itself to one species of plant, visit flowers of *R. raphanistrum* and *S. arvensis* indiscriminately.

*Subularia aquatica*, L.—When the water is unusually high, the flowers remain closed and submerged, and fertilise themselves (17, 351).

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#### REVIEW OF THE CRUCIFERÆ.

With great uniformity in the general structure of the flower, Crucifers show such variability in the number and position of the honey-glands and in the situation of the anthers in relation to these and to the stigma, that scarcely two of the species that we have discussed agree fully in these points.

The number of honey-glands may be two, four, or six; they are placed on or between the bases of the stamens: and in the former case, either on their inner side, their outer side, or round about them; intermediate positions are sometimes assumed by abortive and functionless glands. The honey when secreted either remains in drops upon the glands or fills spaces between the stamens and pistil or accumulates in sepaline pouches.

All or certain of the anthers are placed so that honey-seeking insects must touch them with one side and the stigma with the other; but their situation is not always the most favourable for this result, and the more they diverge from the position most favourable to cross-fertilisation, the more chance do they give of self-fertilisation.

This is explained by the following circumstances.

In all the Cruciferæ which we have considered, the position of the anthers in relation to the honey-glands and the stigma renders cross-fertilisation likely, but not by any means inevitable, on the visit of a honey-seeking insect; but it does not in any way favour cross-fertilisation more than self-fertilisation if the insect comes to feed on or gather pollen. The abundance as well as the diversity of insect-visitors is not great in the species we have considered; we find chiefly flies (especially *Syrphidæ*), bees (especially the less specialised forms), and in less degree other *Hymenoptera* (especially *Sphegidæ*), *Coleoptera*, and *Lepidoptera*. *Hesperis tristis* is

alone adapted for nocturnal insects, and *Pringlea* has become anemophilous in the absence of insects suitable for its fertilisation. On the whole, Crucifers are far behind Umbellifers in the number and variety of their insect-visitors, both on account of their less conspicuous flowers and their less accessible honey; and not rarely plants remain altogether unvisited. The possibility of self-fertilisation is useful if not necessary for the preservation of all the Crucifers that we have considered; in many we find that self-fertilisation takes place to a very considerable extent; and in several we have experimental evidence that it is productive of seed. Under these circumstances it would be better for the plant to forego attaining in its anthers the most favourable position possible for dusting honey-seeking insects with pollen, if by doing so, while retaining the chance of cross-fertilisation if insects did come, it could fully insure self-fertilisation if they did not.

It is impossible, therefore, to consider with Hildebrand that the twisting of the stamens in Crucifers is "a remarkable expression of repugnance to self-fertilisation" (351, p. 48); it rather refers solely, as Axell rightly explains, to the dusting of insects with the pollen on their way to the honey (17, p. 19). But even Axell's statement needed correction and completion, since he only acknowledged two distinct cases in the arrangement of the honey-glands and the twisting of the stamens, and referred all Cruciferae to one or other of these two types; and further, he did not take the position of the anthers into account as an aid to self-fertilisation.

The way in which conspicuousness is attained throughout the Umbelliferae by association of many flowers in one surface, and by asymmetrical development of florets for the common good, is exemplified only in isolated genera of Cruciferae (*Teesdalia*, R. Br., *Iberis*, L.); and, in *Teesdalia* at least, it does not so far insure cross-fertilisation that self-fertilisation may be dispensed with.

#### ORD. CAPPARIDEÆ.

*Capparis*, L., *Cleome*, L., and *Polanisia*, Rafin., are proterandrous, according to Delpino (172, 352).

#### ORD. RESEDACEÆ.

42. RESEDA ODORATA, L.—The receptacle is raised up between the petals and stamens in the upper half of the flower into a perpendicular quadrangular plate, velvety on its anterior surface,

which is yellowish during the time of flowering and orange-red afterwards. It serves as a guide towards the honey, which is secreted and lodged upon the smooth green posterior surface.

The expanded claws of the upper and middle petals lie close to the hinder surface of this plate and surround its upper and

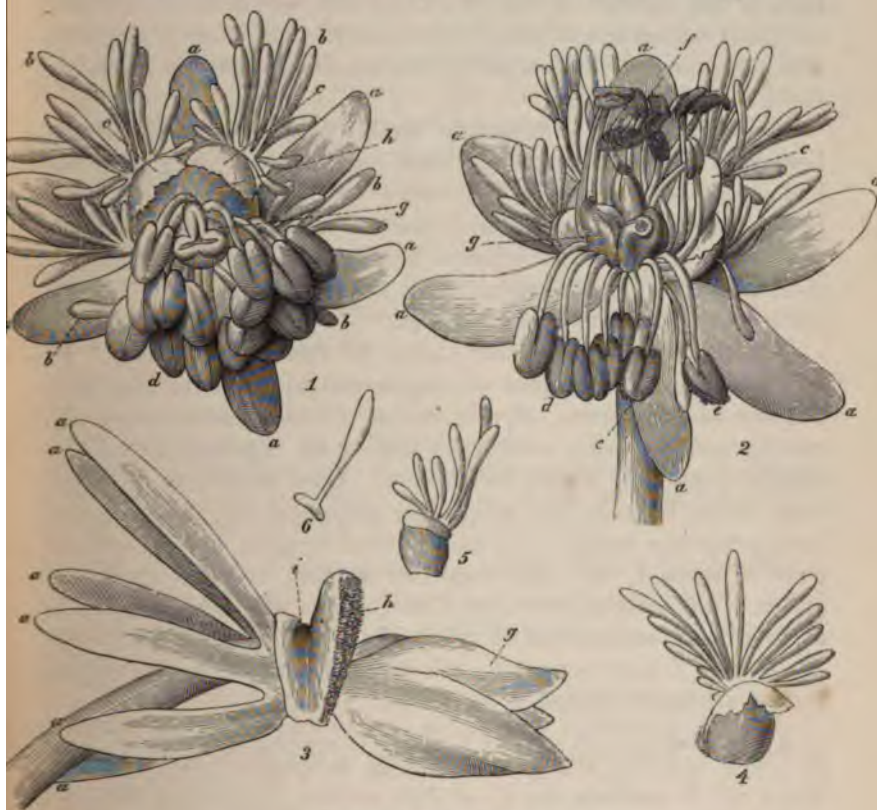


FIG. 35.—*Rereda odorata*, L.

- 1.—Flower before the anthers have dehisced, seen from the front.
- 2.—Ditto after some of the anthers have dehisced.
- 3.—Young fruit in side view.
- 4.—Left superior petal.
- 5.—Left lateral ditto.
- 6.—Left inferior ditto.

a, sepal; b, petal; c, expanded claws of the superior and lateral petals, which surround the shield-shaped swelling of the disc (h); d, anther bent downwards, not yet dehiscent; e, anther dehiscent and rising up; f, anther dehiscent and erect; g, pistil; h, shield-shaped swelling of the disc; i, nectary and honey.

lateral borders with *their* anteriorly directed lobes, thus protecting the honey *effectually* both from rain and from useless visitors (flies). The *laminae* of these petals, which are split into white, radiating, club-shaped strips, assist the red anthers in

making the flower conspicuous. It is also rendered perceptible at a distance by its powerful scent.

There is no true expansion of the flower, since its parts lie open even in the bud: the commencement of the flowering-period is marked rather by the honey-glands beginning to secrete, and by some of the anthers (1, Fig. 35), which had been bent down under the pistil, dehiscing and rising up towards the honey-secreting plate, while the three or four carpels at the same time develop stigmatic papillæ at their apices.

Since the pistil projects considerably from the middle of the horizontal flower, it forms the most convenient landing-place for honey-seeking insects, and is hence very readily covered with pollen from other flowers. In default of insect-visits self-fertilisation takes place, as the stigmas lie immediately underneath the erect anthers. Plants which were kept protected from insects yielded capsules filled with good seed.

The flowers are especially visited by species of *Prosopis*. In July, 1867, I had some pots of mignonette in flower in the open window of my room. Specimens of *Prosopis* kept constantly coming and fluttering, sometimes five or six together, in an unusually lively way about the flowers. They sometimes plunged their heads between the shield-like plate and the upper petals, licking up the honey with outstretched tongue, and sometimes gnawed through the still unopened anthers and devoured the pollen. In subsequent years I have repeatedly observed these actions on *R. odorata* and *R. luteola*, L., both cultivated and wild. Altogether I have noted the following insects as visitors of our species of *Reseda*, including *R. odorata*.

A. Hymenoptera—(a) *Apidæ*: (1) *Prosopis communis*, Nyl. ♀ ♂, very ab.; (2) *P. armillata*, N. ♀ ♂; (3) *P. signata*, Pz. ♀ ♂, ab.; (4) *P. pictipes*, Nyl. ♂; (5) *P. annularis*, Sm. ♀; (6) *Apis mellifica*, L. ♀, ab., s. and c.p.; (7) *Halictus zonulus*, Sm. ♀ c.p.; (8) *H. Smeathmanellus*, K. ♀ c.p.; (b) *Sphegidae*: (9) *Cerceris variabilis*, Schrk. ♀ ♂, s. and f.p. B. Diptera—*Syrphidæ*: (10) *Syritta pipiens*, L., f.p. C. Thysanoptera—(11) Thrips, very ab.

#### 43. RESEDA LUTEOLA, L. :—

Hymenoptera—*Apidæ*: (1) *Prosopis armillata*, Nyl. ♀ ♂, ab.; (2) *P. communis*, Nyl. ♀ ♂, very ab., s. and f.p.; (3) *Apis mellifica*, L. ♀, s. and c.p.; (4) *Andrena nigroænea*, K. ♀, s. See also 590, II.

#### 44. RESEDA LUTEA, L. (Thuringia) :—

Hymenoptera—(a) *Sphegidae*: (1) *Cerceris arenaria*, L., scarce; (2) *C. labiata*, F., ab.; (3) *C. variabilis*, Schrk., very ab.; (b) *Vespidæ*: (4) *Odynerus parietum*, L. ♂, all sucking.

## ORD. CISTINEÆ.

45. *HELIANTHEMUM VULGARE*, L. (Sauerland).—The flower has three sepals, five petals which spread out to face the sun, and many more than 100 stamens whose anthers mature simultaneously with the large capitate stigma. The stigma slightly overtops the anthers, which at first stand close around the centre of the flower, but move outwards when touched, dusting the insect that touches them with pollen. The result of this irritability of the stamens is that the flower is most conveniently approached from the outside, *i.e.* from the corolla, by the first visitor, and at least as conveniently from the centre by subsequent visitors. If an insect which has been dusted with pollen in the first flower alights in the middle of the next, it always effects cross-fertilisation. In default of insect-visits, self-fertilisation results in the closed and slightly nodding flowers. The flower contains no honey, for which the excess of pollen is some compensation.

Visitors: A. Diptera—*Syrphidæ*: (1) *Helophilus pendulus*, L.; (2) *Syrphus pyrastris*, L.; (3) *S. ribesii*, L.; (4) *Melithreptus scriptus*, L.; (5) *M. tæniatus*, Mgn.; (6) *Ascia podagrica*, F., all f.p. B. Hymenoptera—*Apidæ*: (7) *Apis mellifica*, L. ♀, ab.; (8) *Bombus muscorum*, L. ♀; (9) *Halictus villosulus*, K. ♀; (10) *Andrena fulvicrus*, K. ♀, all c.p. C. Coleoptera—*Cerambycidæ*: (11) *Strangalia nigra*, L., devouring the anthers.

On the Alps I have found *H. vulgare* visited by fifty-three species of insects; the small-flowered *H. alpestre* by fourteen. They were mostly *Diptera*, *Apidæ*, and *Coleoptera*, but in part also *Lepidoptera* (609).

Most North American species of *Helianthemum* produce, in addition to the ordinary flowers, much more numerous cleistogamic ones. The same occurs in the case of *H. Kahiricum* and *H. Lippii* in Egypt (531).

The flowers of *H. guttatum* only open in the morning and close after a few hours, fertilising themselves if cross-fertilisation has not meanwhile taken place. The same is the case in *H. villosum*, Thib., *H. ledifolium*, L., *Cistus hirsutus*, L., and *C. villosus*, L. (12).

*Lechea*, L., also bears cleistogamic flowers (399).

## ORD. VIOLARIÆ.

46. *VIOLA TRICOLOR*, L.—The peculiar arrangement of *Viola* was in substance elucidated by Sprengel. Hildebrand subsequently drew attention to the lip-like valve of the stigmatic cavity, by

which cross-fertilisation is assisted in *Viola tricolor*, which had been overlooked by Sprengel. I have observed (No. 570) that this lip, which insures cross-fertilisation, is only developed in the large-flowered variegated variety of *V. tricolor*, while in the small-flowered, whitish-yellow variety, *V. arvensis*, the orifice of the stigma is devoid of a lip and is curved inwards; in this form the flower fertilises itself spontaneously very soon after opening.

In all our violets the spurs of the lower anthers act as honey-glands, and the hollow spur of the lower petal which contains them forms a receptacle for the honey. To reach the honey in *Viola tricolor*, the insect must thrust its proboscis into the flower close under the globular head of the stigma. This lies in the anterior part of a groove, fringed with hairs, on the inferior petal. The anthers, which together form a cone, shed their pollen into this groove, either of themselves or when the pistil is shaken by the insertion of the bee's proboscis. The proboscis, passing down this groove to the spur, becomes dusted with pollen; as it is drawn back it presses up the lip-like valve so that no pollen can enter the hollow stigmatic chamber; but as it enters the next flower it leaves some pollen on the upper surface of the valve, and thus cross-fertilisation is effected.

I have observed very numerous bees visiting a handsome, large-flowered variety which is not uncommon on sandy soil at Lippstadt, growing along with *V. arvensis*. *Apis mellifica*, L. ♀, always sucks in a reversed position with its head downwards; it often alights in the usual position and then turns round. Humble-bees usually suck hanging back downwards to the flowers, which are bent down by their weight. *Bombus terrestris* (7 to 9) and *B. lapidarius* (12 to 14) usually turn round, so as to introduce their proboscis in the same way as the honey-bee. *B. hortorum* (18 to 21) and *Anthophora pilipes* (19 to 21) grasp the flower from behind with their forefeet, and insert their tongues from below in an opposite direction to the honey-bee (590, II.).

*Andrena albicans*, K. ♂, made efforts to suck honey, thrusting its proboscis repeatedly into the same flower. The attempt must have been fruitless, as the proboscis of this bee is only 2 to 2½ mm. long, while the pollen-collecting groove described above is 3 mm. long, and the spur extends for another 3 mm.; in this case, the repeated insertion of the proboscis into the same flower must have led to self-fertilisation. I repeatedly noticed a common small fly, *Syrphia pipiens*, L., eating pollen in the groove and on the anthers of *V. tricolor*; as it often touched the stigma also with its

proboscis, it might easily accomplish self-fertilisation. Delpino saw *V. tricolor* visited by *Anthophora pilipes*. Darwin found it visited by *Bombus* sp. and *Rhingia rostrata*.

I have found *V. tricolor*, var. *arvensis*, to be very sparingly visited, chiefly by bees and humble-bees, more rarely by *Rhingia* and by butterflies (590, II.).

*Viola calcarata*, L., greatly surpasses *V. tricolor* in the size of its flower and the length of its spur (13 to 25 mm.). It is fertilised only by Lepidoptera, chiefly by *Macroglossa stellatarum* (25 to 28 mm.), our quickest worker. I have seen this insect visit 194 flowers on different plants in 6½ minutes, and I could see it cross-fertilise them by means of the tip of its proboscis dusted with white pollen (609).

*Viola cornuta*, according to Mr. W. E. Hart (308), is adapted for fertilisation by nocturnal Lepidoptera by its long spur and by emitting its perfume most powerfully by night. He found it visited by humble-bees, by *Hipparchia Janira*, and by *Cucullia umbratica*.

*Viola arenaria*, D.C., is visited by butterflies (609).

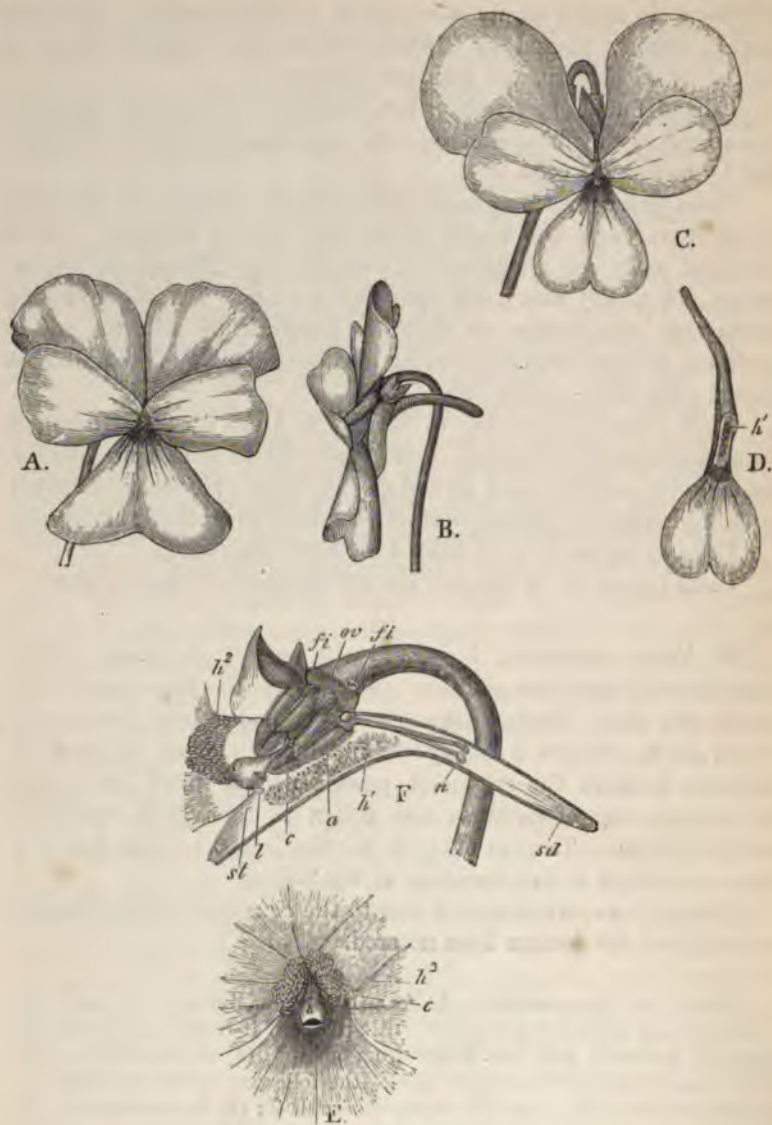
*Viola biflora*, L., is adapted for fertilisation by Diptera (609).

47. VIOLA ODORATA, L.—Here the end of the pistil which bears the stigma is not globular and close to the lower petal, but stands at a short distance from the latter and is bent downwards into a hook. When a honey-seeking insect thrusts its head or proboscis beneath the stigma it pushes up the pistil and opens the conical ring of anthers; the pollen is thus shed upon the inserted organ. Thus in every flower the insect touches first the stigma and then causes shedding of the pollen.

Sprengel's experiments led him to the conclusion that if insects are excluded the flowers bear no seed.

Visitors : A. Hymenoptera—*Apidae* : (1) *Apis mellifica*, L. ♀, very ab., s. (as Sprengel described and figured (title-page xi.) it comes downwards and inserts its proboscis into the flower from above); (2) *Anthophora pilipes*, F. ♂, sucks, clinging to the lower petal,—the following species do likewise; (3) *Bombus hortorum*, L. ♀; (4) *B. lapidarius*, L. ♀; (5) *B. Rajellus*, Ill. ♀; (6) *Osmia rufa*, L. ♂ ♀, very ab., also enters the flower from above as a rule. B. Diptera—*Bombylidae* : (7) *Bombylius discolor*, Mgn., s. C. Lepidoptera—(8) *Vanessa urticae*, L., s.; (9) *Rhodocera rhamni*, L., s.

48. VIOLA SILVATICA, Fries. (*V. silvestris*, Lam.).—The spur is 7 mm. long; the honey-secreting appendages to the inferior anthers which project into it are 5 mm. long. As in *V. tricolor*, the cavity

FIG. 36.—*Viola calcarata*, L.

- A.—Front view of flower, from Piz Umbrail, nat. size.  
 B.—Ditto, lateral view (July 16, 1875).  
 C.—Front view of flower, from Albula, nat. size.  
 D.—Lip of ditto. with its spur (August 2, 1876).  
 E.—Front view of the mouth in A ( $\times 3\frac{1}{2}$ ).  
 F.—Section of A, after removal of the greater part of the corolla ( $\times 3\frac{1}{2}$ ).  
 a, anthers; c, appendages of the connectives;  $h'$ , pollen-collecting hairs;  $h^2$ , hairs which in species of *Viola* fertilised by bees aid the bee in clinging to the flower, here preserved as a functionless hereditary character; k, stigma; l, lip on the under side of the entrance to the cavity of the stigma (st); sd, honey receptacle; fl, filaments; ov, ovary.

of the stigma is protected by a lip-shaped valve; but the pollen is shed directly upon the insect's proboscis or head, as in *V. odorata*.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus agrorum*, F., ♀, s. B. Diptera—*Bombylidæ*: (2) *Bombylius discolor*, Mgn. s. C. Lepidoptera—(3) *Anthocharis cardamines*, L., s.; (4) *Pieris brassicæ*, L.; (5) *P. napi*, L., s.; (6) *P. rapæ*, L., s.; (7) *Rhodocera rhamni*, L., s.

#### 49. VIOLA CANINA, L. :—

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus lapidarius*, L. ♀, s.; (2) *Osmia rufa*, L. ♂, s.; (3) *O. fusca*, Chr. ♀, s. B. Diptera—*Bombylidæ*: (4) *Bombylius major*, L., s. C. Lepidoptera—*Rhopalocera*: (5) *Pieris rapæ*, L., s.; (6) *P. napi*, L., s.

Cleistogamic flowers have been observed in many *Violarieæ*: in *V. mirabilis*, L., by Dillenius; in *V. pinnata*, L., and *V. montana*, L., by Linnæus; in *V. elatior*, Fr., *V. pumila*, var. *lancifolia*, Thor.; *V. odorata*, L., and *V. canina*, L., by Daniel Müller; in *Ionidium*, Vent., by Bernouilli. I can add *V. bicolor*<sup>1</sup> to this list. In the summer of 1859, I gathered some plants of this species at Ramsbeck Waterfall, and placed them in a plate with water under the shadow of a bush in my garden, to let the flowers expand; the plants, which I watched daily, grew well, and though no flowers opened I obtained plenty of capsules with good seed. Cleistogamic flowers have been seen by Mr. T. H. Corry in *V. silvatica*, Fries., and in *V. stagnina*, Kit.; they are rare in the latter. Bennett has observed cleistogamic flowers in *Viola cucullata*, Ait., *V. silvatica*, *V. floribunda*, and *V. sagittata*, Ait. (79).

#### EVOLUTION OF COLOUR IN VIOLETS.

Various facts show that the flowers of the Violet were originally yellow.

The smallest, most short-spurred of our *Violas* is *V. biflora*, which is visited by Diptera, and only exceptionally by short-lipped bees; its flowers are yellow. The smallest-flowered form of *V. tricolor* (var. *arvensis*) has whitish-yellow flowers. The large-flowered *V. tricolor*, var. *alpestris*, shows all stages in the passage from yellow flowers to blue; many plants have flowers which are yellow throughout, in others the flowers are yellow when they

<sup>1</sup> *V. bicolor*, Pursh., is a form of *V. tricolor*, var. *arvensis*.—Asa Gray, *North American Flora*.

open, but change gradually to blue, and in others the change to blue occurs immediately after opening, or even before.

The most specialised form, *V. calcarata*, is almost always blue, but occasionally it reverts to the ancestral yellow colour (609).

#### ORD. POLYGALÆÆ.

50. *POLYGALA COMOSA*, Schk.—The structure of the flower of *P. vulgaris*, which agrees in all essential points with that of *P. comosa*, here figured, was first explained by Hildebrand (352).

The two lateral sepals (*alæ*), which are large and coloured, render the flower conspicuous. The inferior petal (*p'*) is furnished

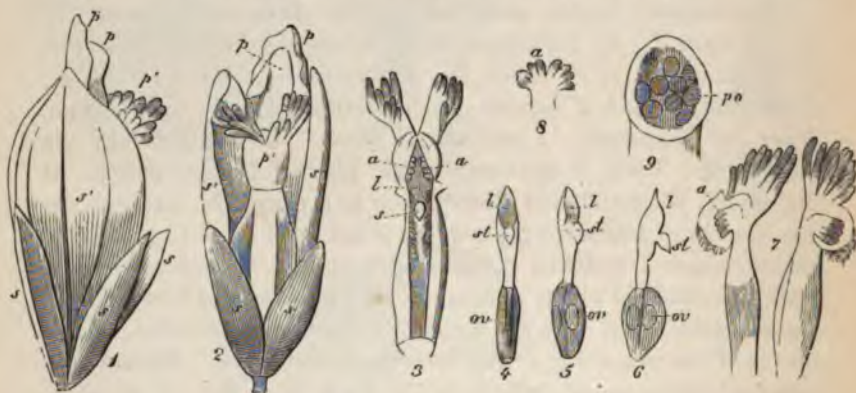


FIG. 37.—*Polygala comosa*, Schk.

1.—Flower in side view (the flower should naturally be horizontal). *s*, sepal; *p*, petal; *s'*, one of the two lateral sepals which play the part of a corolla; *p'*, anterior petal, provided with digitate appendages, to which the insect clings.

2.—Flower, from below.

3.—Anterior petal, with the essential organs inclosed in it, from above. *a*, anthers; *s*, stigma, which applies sticky matter to the insect's proboscis passing over it; *l*, spoon-shaped end of the style, which receives the pollen issuing from the anthers.

4.—Pistil, from above.

5.—Ditto, seen obliquely from above.

6.—Ditto, in side view.

7.—Anterior petal of a flower just about to expand, split to show the anther inclosed by it.

8.—The united anthers.

9.—An anther dehiscent. *po*, pollen-grains.

at its apex with finger-like processes, which support the bee when it alights. On the upper surface of this petal is a pouch with two valves, inclosing the essential organs; in it lies the spoon-shaped style with its concavity upwards, and in this the anthers on both sides lie and shed their pollen; close behind its hollow extremity the style bears a viscid stigmatic lobe, bent sharply downwards. An insect which tries to reach the honey secreted in the base of the flower must, while clinging to the fimbriate processes

of the lower petal, thrust its proboscis between the two valves of the pouch, and thus come in contact both with the pollen and with the viscid stigma; the proboscis being thus rendered adhesive carries some pollen with it out of the flower, and when it is drawn out of the next flower in a similar manner it leaves some of this pollen either caught by the stigmatic hook or adherent to the papillæ. Thus cross-fertilisation goes on regularly. In default of insect-visits the stigmatic lobe curves over upon the pollen accumulated in the "spoon," and is thus self-fertilised.

On the Alps *P. comosa* is visited by Lepidoptera, but in Low Germany chiefly by bees (590, II.; 609).

*Polygala alpestris*, Rchb., is visited by butterflies (609).

#### 51. *POLYGALA VULGARIS*, L.:—

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus terrestris*, L. ♀, s., very frequent; (2) *B. lapidarius*, L. ♀, s.; (3) *Apis mellifica*, L. ♀, s. B. Lepidoptera—(4) *Polyommatus Eurydice*, Rott. (*Chryseis*, W. V.), s. See also No. 590, II.

*Polygala Chamæbuxus*, L.—The pollen is stored in a cup at the end of the style, beside which is the sticky stigma-disc (360).

The mechanism of fertilisation shows a certain resemblance to that of *Papilionaceæ*. In both, the stamens and style lie in the inferior part of a tubular horizontal flower, at the end of which they bend upwards, and bear the anthers and stigma. Those parts lying in the anterior part of the flower are in both sheltered by a *carina* formed of coherent petals, and emerge, or at least permit the stigma and pollen to emerge, when the carina is pressed down, as it is by every insect which obtains the honey in the legitimate manner.

In *Polygala Chamæbuxus*, as in *Lotus* and several other *Papilionaceæ*, it is not the anthers themselves that emerge when the carina is depressed, but only part of the pollen which escapes; and after repeated depressions the stigma also emerges, and cross-fertilisation is thus insured. A full description of this interesting flower is given in my book *Die Alpenblumen*.

*Polygala myrtifolia*, L., has also, according to Delpino, a floral arrangement comparable to that of *Papilionaceæ*. The two upper petals represent the vexillum; the lower one represents the carina, and like it surrounds the reproductive organs and allows them to

protrude on being pressed down by the weight of an insect: serrate processes on the lower petal supply the place of alæ. The stamens cohere, forming a tube incomplete superiorly, where a longitudinal split admits the insect's proboscis to the nectaries

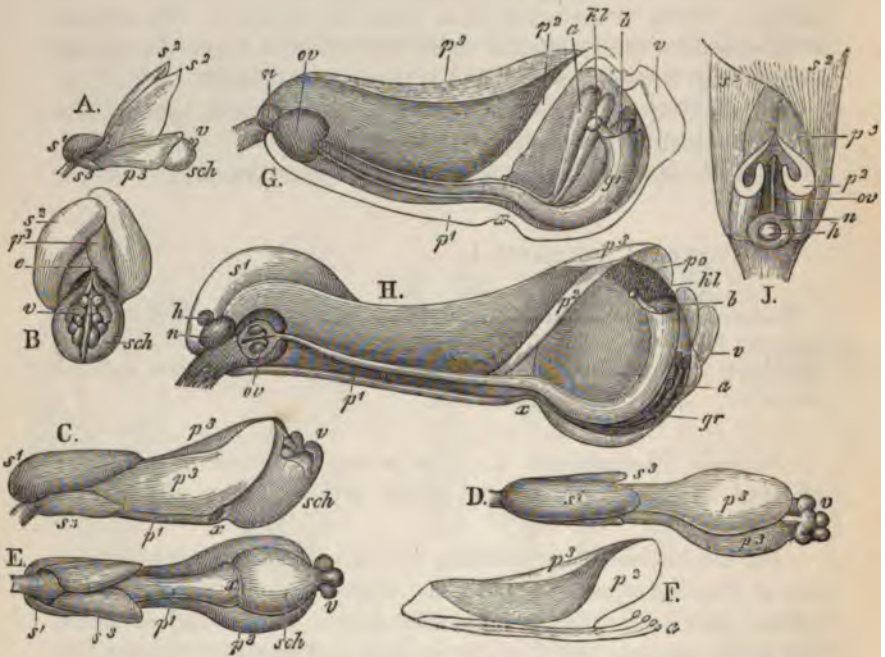


FIG. 38.—*Polygala Chamæbuxus*, L.

- A.—Flower, from the side, natural size.  
 B.—Ditto, front view ( $\times 2\frac{1}{2}$ ).  
 C.—Flower, after removal of the two alar sepals.  
 D.—Ditto, from above.  
 E.—Ditto, from below ( $\times 3$ ).  
 F.—The two petals of the left side, separated from the inferior petal to which they naturally cohere; inner view ( $\times 2\frac{1}{2}$ ).  $p^1$ , superior petal;  $p^2$ , lateral ditto, to which the filaments adhere.  
 G.—Bud in section after removal of the calyx ( $\times 5\frac{1}{2}$ ).  
 H.—Full-grown flower in section ( $\times 5\frac{1}{2}$ ).  
 I.—Base of flower, from the front, after removal of the superior sepal ( $\times 7$ ).  $s^1$ , superior,  $s^2$ , lateral,  $s^3$ , inferior sepals;  $p^1$ , inferior petal;  $p^2$ , lateral ditto, completely united with  $p^3$ , superior ditto. The anterior part of the inferior petal serves as a carina, and rotates by means of a hinge,  $a$ , upon the posterior part;  $b$ , cup at end of style;  $e$ , entrance of the flower;  $kl$ , adhesive matter on the stigma.

surrounding the base of the column. The flowers have the same want of symmetry as those of *Lathyrus* and *Phaseolus*, and are fertilised in the same way by *Xylocopa violacea* (178, 360).

*Polygala* has cleistogamic flowers, according to Kuhn (399).

## ORD. CARYOPHYLLÆ; a. SILENÆ.

52. *DIANTHUS DELTOIDES*, L.—The stamens and petals spring from an annular ridge of the receptacle encircling the stalk of the ovary. This ridge bears on its inner border a yellow fleshy cushion which secretes honey.

The pistil, the stamens, and the claws of the petals, which are grooved to inclose the five inner stamens, are all closely surrounded by the tube of the calyx, which is 12 to 14 mm. long, and a little over 2 mm. wide. A very narrow passage is thus left,

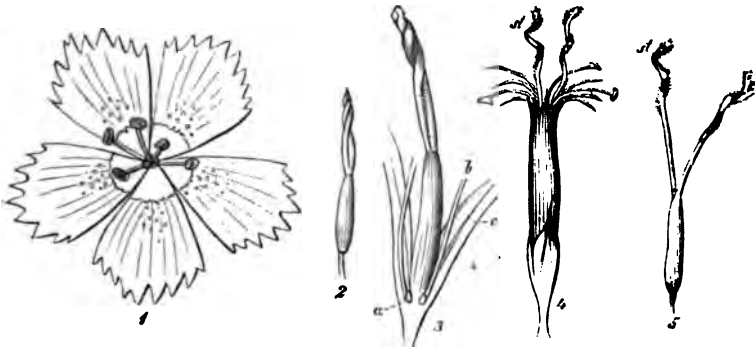


FIG. 39.—*Dianthus deltoides*, L.

1.—Flower in first stage, viewed from above. Five anthers, covered with pollen, protrude from the flower; two that have not yet dehisced are visible in the mouth of the tube.

2.—Pistil at close of the first stage, after all the ten anthers have dehisced. The two styles are still twisted together.

3.—Ditto, with the base of the petals and stamens, more magnified. *a*, nectary, surrounding the base of the ovary as a fleshy ridge; *b*, filaments; *c*, petals.

4.—Flower in second stage, after removal of the petals. Most of the anthers have fallen off, st. stigma.

5.—Pistil in second stage. The two styles have separated, but each retains its spiral twist, so that stigmatic papillæ are turned towards all sides.

12 to 14 mm. long, leading to the honey, which is lodged between the base of the stamens and the ovary. This passage is, in the first state of the flower, so much blocked by the five inner anthers, that the honey is only accessible to the proboscis of Lepidoptera. The flowers are thus specially adapted for butterflies; but their protruding anthers are taken advantage of by pollen-seeking insects which act as subsidiary fertilisers.

Flowering begins by the petals, hitherto erect and involute, spreading out horizontally; they are rose-red, with slightly indented purple transverse lines near the base, and speckled externally to these transverse lines with small white spots, each

of which bears an upright hair. The limb of the corolla forms a rosy circle, finely notched at its circumference, indented by five deep incisions, and with its white centre surrounded by a purple ring, outside which are scattered white spots (Fig. 39, 1). As soon as the flower has expanded and thus made itself attractive to the eminently colour-loving butterflies, the stamens, with their anthers coated all round with pollen, elongate and protrude one after another in rather quick succession from the narrow tube, so that every butterfly which inserts its proboscis must dust at least its head with pollen. The five inner stamens still remain in the tube, rendering it too narrow for anything save the butterfly's proboscis. As the outer stamens wither, the five inner ones protrude in succession; but the two styles still lie twisted together within the tube (Fig. 39, 2 and 3). Only after the stamens have withered, and have for the most part lost their anthers, do the styles elongate and allow the stigmas to emerge from the flower; the stigmas now spread apart, still retaining their spiral twist, so that from whichever side a butterfly comes to suck honey it cannot fail to touch some part of the stigmatic papillæ with its head.

Pollen-seeking insects, if they only resort to young flowers whose anthers still have pollen, cannot act as fertilisers; but they may do so if they alight, as flies often do, upon older flowers with mature stigmas, in which case they fly away again disappointed.

Self-fertilisation is completely prevented by the well-marked dichogamy.

As normal fertilisers of *Dianthus deltoides*, I have only observed *Pieris rapæ*, L., and *Satyrus Janira*, L., but these I have noted repeatedly. Several *Syrphidæ*, viz., *Rhingia rostrata*, L., *Melithreptus scriptus*, L., *M. pictus*, Mgn., and *Helophilus pendulus*, L., resort to the flower for the sake of pollen. I once noticed *Rhingia rostrata* make a vain attempt to reach the honey; it plunged its proboscis with a great effort into four flowers successively, but as its proboscis is only 11 mm. long it never reached the honey; in a short time it resigned the attempt, and betook itself to eating pollen.

53. *DIANTHUS CARTHUSIANORUM*, L., has the same floral mechanism as the preceding species. In Thuringia I have observed numerous visitors upon its flowers, consisting almost solely of Lepidoptera.

(a) *Rhopalocera*: (1) *Colias hyale*, L., frequent; (2) *Rhodocera rhamni*, L., very ab.; (3) *Polyommatus Phléas*, L.; [(4) *Hesperia*, frequent; (b)

*Sphinxes*: (5) *Macroglossa stellatarum*, L.; (6) *Zygæna carniolica*, Scop.; (c) *Noctuæ*: (7) *Plusia gamma*, L., ab.—The only other insect that I have found on the flowers was a small *Halictus*, c.p. (Sept. 1871). See also No. 590, II.

54. *DIANTHUS CHINENSIS*, L.—I have seen flowers in my garden repeatedly visited by *Noctuæ*: (1) *Plusia gamma*, L.; (2) *Agrotis pronuba*, L.; and (3) *Brotolamia meticulosa*, L.

Species of *Dianthus* which I have observed on the Alps (*D. superbus*, L., *D. silvestris*, Wulf., and *D. atrorubens*, All.), are, like the three preceding species, distinctly protogynous, and visited by diurnal *Lepidoptera* (609).

As in the protogynous *Alsineæ*, gynodioecism seems to be widespread in the genus *Dianthus*. It occurs in *D. superbus*,

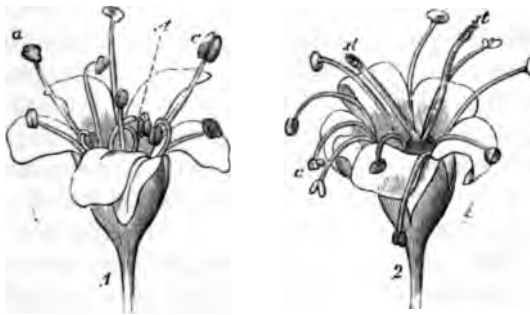


FIG. 40.—*Gypsophila paniculata*, L.

1.—Flower in first (male) stage.

2 Ditto in second (female) stage.

*D. carthusianorum*, and *D. deltoides*, and the last of these shows all gradations between hermaphrodite, gynomonœcious, and gynodioecious flowers (607).

55. *GYPSOPHILA PANICULATA*, L.—Although the corolla, when fully expanded, is barely 4 to 5 mm. in diameter, the many hundreds of flowers borne at once by a single plant, and the abundant and easily accessible honey and pollen, attract numerous insects. The power of self-fertilisation has been entirely lost.

The honey lies between the ovary and a green fleshy ring at the base of the ten stamens; the cup at the bottom of which it lies is  $2\frac{1}{2}$  mm. deep, and about the same in width at the entrance. The honey is therefore accessible to short-lipped insects. First the five outer stamens, which alternate with the

petals, and afterwards the inner five, ripen and protrude from the flower with an inclination outwards. They wither, curving outwards and downwards, and then the two short styles, hitherto bent inwards, elongate and protrude from the flower, diverging from one another.

Visitors: A. Diptera—(a) *Tabanidæ*: (1) *Chrysops cæcutiens*, L., s.; (b) *Syrphidæ*: (2) *Eristalis æneus*, L.; (3) *E. nemorum*, L.; (4) *E. arbutorum*, L., all three ab., s. and f.p.; (5) *Syritta pipiens*, L., very ab.; (6) *Ascia podagrica*, F.; (7) *Syrphus balteatus*, Deg.; (8) *Melithreptus pictus*, Mgn.; (9) *M. tæniatus*, Mgn., all s. or f.p.; (c) *Muscidæ*: (10) *Pyrellia cadaverina*, L.; (11) *Onesia floralis*, Rob. Desv.; (12) *Sarcophaga carnaria*, L.; (13) *Lucilia silvarum*, Mgn., all s.; (14) *Anthomyia* sp.; (15) *Sepsis*. B. Hymenoptera—(a) *Evaniidæ*: (16) *Fænus jaculator*, F.; (b) *Formicidæ*: (17) several species; (c) *Sphegidæ*: (18) *Oxybelus uniglumis*, L.; (d) *Vespidæ*: (19) *Odynerus simplex*, F.; (20) *O. parietum*, L.,—all the Hymenoptera s.

*Gypsophila repens*, L., when flowering on sunny slopes of the Alps where insects are plentiful, is so distinctly proterandrous that spontaneous self-fertilisation is impossible. In less favourable localities it fertilises itself when not visited by insects (609).

*Saponaria ozymoides*, L., is distinctly proterandrous, and is frequented by butterflies. It clothes sunny gravelly slopes in the sub-alpine region with its handsome red flowers. I saw it visited by thirty-three species of Lepidoptera, twenty-eight of which were butterflies, besides some humble-bees and *Bombylidæ*.

*Saponaria vaccaria*, L., is also fertilised by butterflies (590, II.).

56. *SAPONARIA OFFICINALIS*, L.—This species is adapted for nocturnal Lepidoptera, as the foregoing species of *Saponaria* and *Dianthus* are for the diurnal forms. The bright colour and elegant markings which attract butterflies are absent: the flowers are of one colour, and their scent is strongest in the evening. As in the other species, the honey lies hidden in the base of a long narrow tube. The calyx-tube is 18 to 21 mm. long, but the claws of the petals stand a few millimetres higher. The flowers are markedly proterandrous. First, the five outer stamens protrude a few millimetres from the flower, and dehisce immediately over its entrance; afterwards they spread apart and leave the entrance free. The five inner stamens now follow the same course, turning, as the others did, the pollen-covered surface of their anthers upwards. The styles are still inclosed within the tube, and are only slightly separated at their apices. When the inner stamens have withered, the two styles grow up out of the flower, and spread apart, turning

their papillar inner surfaces upwards. The honey is secreted as in *Dianthus*. I omitted to watch the flowers in their season, and can only mention *Sphinx ligustri*, L., as a fertiliser; it visited the flowers of this plant in my garden one evening during slight rain, and sucked them with the usual rapidity of the hawk-moths. I have also found *Halictus morio*, F. ♀, collecting pollen on the flowers (July 13, 1869).

*Silene rupestris*, L., is proterandrous, and is visited by numerous insects. It inhabits the same localities as *Gypsophila repens*, and secretes and conceals its honey in the same way as that species. Its flowers are equally conspicuous, but stand somewhat isolated on sparingly branched stalks; owing probably to this circumstance, the power of self-fertilisation has not been entirely lost (609).

*Silene acaulis*, L., ascends in the higher Alps to a height of over 10,000 feet. Its low tufts closely studded with pink or carmine flowers attract so many butterflies that as a rule the plant has been able to dispense with the power of self-fertilisation. Most tufts are exclusively staminate or pistillate, and only rarely hermaphrodite and proterandrous. The latter in case of need fertilise themselves. I have observed eighteen species of butterflies on this flower (609).

As *Silene acaulis* is adapted for diurnal Lepidoptera, so *S. inflata*, Sm., and *S. nutans*, L., are adapted for the nocturnal forms. I found both on the Alps, visited in the evening by Noctuidæ, and in the daytime by humble-bees. *Silene nutans*, L., is markedly proterandrous. According to Kerner, each flower opens upon three successive nights, on which the outer stamens, the inner stamens, and the stigmas are exerted respectively. According to Ricca (665), the flowers are sometimes diclinous by incomplete development of the stamens, that is to say, gynodioecious. *Silene inflata*, L., is tricecious and polygamous, like *S. acaulis*.

*Lychnis flos-Jovis*, L., is distinctly proterandrous; *L. rubra*, Weigel, is tricecious and polygamous. Both have bright red flowers, and are greatly frequented by butterflies on the Alps (609).

*Lychnis Viscaria*, L., is also adapted for cross-fertilisation by butterflies (590, II.).

*Lychnis alpina*, L.—The proterandrous flowers are figured and described by Axell (17).

57. *LYCHNIS FLOS-CUCULI*, L.—In regard to the position of the honey, the flowers of this plant are intermediate between

those of *Stellaria*, *Cerastium*, and *Gypsophila paniculata*, where the honey is fully exposed, and *Dianthus* and *Saponaria*, where it is only accessible to Lepidoptera. The insect-visitors include bees, Lepidoptera, and some long-tongued flies. The nectaries, which lie at the base of the stamens, cohere into a fleshy ring surrounding the ovary. The calyx tube is 6 to 7 mm. long, and bears teeth 3 mm. long, which stand erect and support the claws of the petals. The honey is thus accessible to insects which have a proboscis 9 to 10 mm. long; or which, with a proboscis at least 6 mm. long, have strength enough to push apart the claws of the petals, above the level of the calyx-tube; or, finally, to insects small enough to creep down the tube.

The flowers are distinctly proterandrous. First, the five outer anthers dehisce, while standing in the entrance of the flower and having their pollen-covered sides turned towards one another. The tube, though it permits a butterfly's proboscis to pass easily down, is so much obstructed by the anthers that the proboscis cannot fail to be dusted with pollen. These stamens then elongate, and bend outwards to lie in the intervals between the petals, while the inner whorls take their place in the entrance of the flower. When these wither, the five styles grow up, and the stigmatic papillæ, which clothe the whole of their inner surfaces, attain their full development. The styles reach to the entrance of the flower, and their ends make  $1\frac{1}{2}$  to 2 spiral turns, so that an insect cannot fail to touch some part of the stigmatic surfaces with its proboscis in thrusting it down into the flower.

The flowers are chiefly visited for the sake of their honey; I have only seen the hive-bee collecting pollen, and two species of Syrphidæ feeding on it.

Visitors : A. Hymenoptera—*Apidæ* : (1) *Bombus Rajellus*, Ill. ♀ (12 to 13) ; (2) *B. lapidarius*, L. ♀ (10 to 14) ; (3) *B. agrorum*, F. ♀ (12 to 15) ; (4) *B. terrestris*, L. ♀ (7 to 9) ; (5) *Apis mellifica*, L. ♀ (6), ab., s. and c.p. ; (6) *Osmia rufa*, L. ♀ (9) ; (7) *Andrena nitida*, K. ♀ (3 to 4), they sought in vain for honey in several flowers. B. Lepidoptera—(a) *Rhopalocera* : (8) *Pieris brassicæ*, L. (15) ; (9) *P. rapæ*, L., both ab. ; (10) *Lycæna Icarus*, Rott. ; (b) *Sphinges* : (11) *Macroglossa fuciformis*, L. ; (12) *Ino statices*, L. ; (c) *Noctuæ* : (13) *Euclidia glyphica*, L., very ab. C. Diptera—*Syrphidæ* : (14) *Rhingia rostrata*, L. (11 to 12), s. ; (15) *Volucella plumata*, L., f.p. ; (16) *Syrphus pyrastris*, L., f.p.

I have observed the stamens of *L. flos-cuculi* dusted with butterflies' scales, and a *Pieris rapæ* which I caught upon the flower had a number of its pollen-grains among the hairs and scales on the forepart of its head.

58. *LYCHNIS VESPERTINA*, Sibth. (*L. dioica*,  $\beta$ , L.).—The structure of the flower has been thoroughly explained by Sprengel. Honey is secreted by the lower, fleshy part of the (developed or abortive) ovary, and lies at a depth of 20 to 25 mm. in fertile or pistillate flowers, and of 15 to 18 mm. in barren or staminate ones. Both kinds of flowers are much constricted near their upper end by the calyx, and can only be forced open a little at the very brim by an insect's head; a thin proboscis at least 15 to 20 mm. long is needed to reach the honey. The pure white flowers, which have no guiding marks, expand in the evening, though they are not completely shut by day. These characters taken together exclude diurnal insects except such as come seeking pollen, and make the flowers so much the more attractive to crepuscular and nocturnal *Lepidoptera*. According to Delpino (178, p. 161), the anthers ripen two by two, a fact which I have not observed. A further remark of Delpino's, that the flowers stand horizontally, and let the stamens emerge at their highest part, does not at all hold good of the specimens in my neighbourhood, which have an almost perpendicular position, as Sprengel figures them.

I have repeatedly seen *Sphinx porcellus*, L., visiting and cross-fertilising the flower.

59. *LYCHNIS GITHAGO*, L., is, like *Dianthus*, adapted for fertilisation by butterflies, and resembles *Dianthus* in regard to its nectaries, the position of its honey, its proterandrous dichogamy, and the order of development of its anthers (702, p. 254).

Visitors: A. *Lepidoptera*—*Rhopalocera*: (1) *Hesperia silvanus*, Esp., s.; (2) *Pieris brassicae*, L., s., very ab. B. *Diptera*—*Syrphidae*: (3) *Rhingia rostrata*, L., I saw it insert its proboscis repeatedly, seeking in vain for honey. See also No. 590, II.

The species of *Silene* and *Lychnis* have a relation, according to Dr. Buchanan White, to species of *Dianthæcia* (*Noctuidæ*) like that which exists between *Yucca* and the *Yucca*-moth. The species of *Dianthæcia* fertilise *Silene* and *Lychnis*, and thereby make provision for their larvæ, which feed exclusively on the unripe seeds of these plants. But *Silene* and *Lychnis* have many other insect-fertilisers besides (773).

#### ORD. CARYOPHYLLÆ; b. ALSINÆÆ.

60. *CERASTIUM ARVENSE*, L.—The flowers resemble those of *S. Holostea* in the position of their nectaries, in the order of development of the two staminal whorls and the stigmas, and hence also

in the likelihood of cross-fertilisation in case of insect-visits, and of self-fertilisation in their absence. They are equally conspicuous, and are visited to about the same extent.

Visitors : A. Diptera—(a) *Stratiomyidae* : (1) *Stratiomys* sp., s. (b) *Empidae* : (2) *Empis opoca*, F. ; (3) *E. rustica*, Fallen, both very ab., s. ; (c) *Leptidae* : (4) *Leptis strigosa*, Mgn., s. ; (d) *Syrphidae* : (5) *Eristalis nemorum*, L. ; (6) *E. arbustorum*, L. ; (7) *E. sepulchralis*, L. ; (8) *Syritta pipiens*, L., all four ab., s. ; (9) *Platycheirus manicatus*, Mgn., ab., s. ; (10) *Syrphus*, sp., s. ; (11) *Melanostoma mellina*, L., s. ; (e) *Muscidae* : (12) *Sepsis* ; (13) *Anthomyia setiva*, Mgn., s. B. Hymenoptera—*Apidae* : (14) *Andrena argentata*, Sm. ♀, s. ; (15) *A. albicans*, K. ♀, s. ; (16) *Halictus*, ♀ (the size of *H. nitidiusculus*) s. C. Coleoptera—*Staphylinidae* : (17) *Omalium florale*, Pk. D. Thysanoptera : (18) Thrips, frequent in the base of the flower. E. Lepidoptera—(19) *Polyommatus Phloas*, L., s. See also No. 590, II., and No. 609.



FIG. 41.—*Cerastium arvense*, L.

1.—Flower in first stage. The outer whorls of anthers are covered with pollen, the inner are not yet full grown ; the styles are curled inwards.

2.—Flower at the end of the third stage. The outer anthers are in part fallen off, and in part withered ; the inner are still sparingly coated with pollen ; the stigmas are mature.

61. *CERASTIUM TRIVIALE*, Link, has smaller flowers and fewer insect-visitors ; accordingly it is less markedly proterandrous than *C. arvense*. It produces seed by self-fertilisation in the absence of insects (Axell, 17).

Visitors : Diptera—(a) *Syrphidae* : (1) *Syritta pipiens*, L., s. and f.p. ; (b) *Empidae* : (2) *Empis livida*, L., s.

62. *CERASTIUM SEMIDECANDRUM*, L., has still smaller flowers and is still less frequently visited than the preceding species ; it is still less distinctly proterandrous, and fertilises itself regularly in absence of insects.

As in *Stellaria media*, the inner honeyless stamens are usually abortive, but remains of their filaments, sometimes attaining half the length of the outer stamens, frequently remain. When the anthers dehisce, they occupy the middle of the flower, and the stigmas still lie close together, though their tips are bent outwards and easily receive pollen. Later, the anthers pass outwards, the stigmas lengthen slightly and spread out, turning their inner

surfaces, which are covered with long papillæ, upwards. An insect visiting a young flower dusts itself with pollen, and also applies pollen from the same or from another flower to the tips of the stigmas; in an older flower it is likely to dust the outspread stigmas with pollen from another flower; in the absence of insects the stigmas as they curve outwards come in contact with the anthers still covered with pollen.

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Rhingia rostrata*, L., s. (May 10, 1870); (b) *Muscidæ*: (2) *Pollenia vespillo*, F.; (3) *P. rudis*, F., both s. and inserting the proboscis three to five times in each flower (April 17, 1871). B. Hymenoptera—*Apidæ*: (4) *Apis mellifica*, L. ♀,—I saw (April 3, 1871) the honey-bee in great numbers flying over a bare field of *C. semidecandrum*, sucking the tiny flowers by dipping its proboscis once into each.

*Cerastium viscosum*, L., has cleistogamic flowers (40).

63. *MALACHIUM AQUATICUM*, Fries.—The flowers of this plant are more conspicuous than those of *Cerastium triviale* and *C. semidecandrum*, but less so than those of *C. arvense* and *Stellaria Holostea*; in the same intermediate position stands the amount of its insect-visits and its floral arrangement, which favours both cross- and self-fertilisation. The flower is proterandrous, and in absence of insects the ends of its outspread stigmas come in contact with the pollen-covered anthers. The styles vary in number from three to five, the latter number being most frequent, so that *Malachium* here probably resembles the common ancestors of *Cerastium* and *Stellaria*.

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Helophilus lineatus*, F.; (2) *Eristalis arbustorum*, L.; (3) *Syritta pipiens*, L.; (4) *Ascia podagrica*, F., all ab., s.; (b) *Muscidæ*: (5) *Anthomyia* sp., s. B. Coleoptera—*Nitidulidæ*: (6) *Meligethes*, ab., l.h. C. Thysanoptera: (7) *Thrips*, very freq. D. Hymenoptera—*Apidæ*: (8) *Prosopis communis*, Nyl. ♀, s.; (9) *Pr. hyalinata*, Sm. ♀, s.; (10) *Halictus sexnotatus*, K. ♂, s.

64. *STELLARIA GRAMINEA*, L.—The nectaries surround the bases of the five outer stamens as green, fleshy swellings. The flowers exhibit three stages, which, however, merge one into another. In the first period, the five outer stamens curve in towards the middle of the flower, and their anthers dehisce widely, covering themselves all round with pollen; the inner stamens are meanwhile bent outwards, and their anthers are still closed. The styles are not yet fully developed, and are curved inwards with their papillar surfaces directed downwards. The five inner stamens dehisce before the other five have withered, but still remain bent farther outwards; this marks the second stage. As these inner stamens

wither and shrivel up, the styles rise up, and spread outwards turning their papillar surfaces upwards, and curving their ends, also papillar, outwards and downwards (third stage). Every insect which is not too small, whether it alights in the middle of the flower or on one of the petals, must, to reach the nectaries, come in contact with pollen in younger flowers or with the

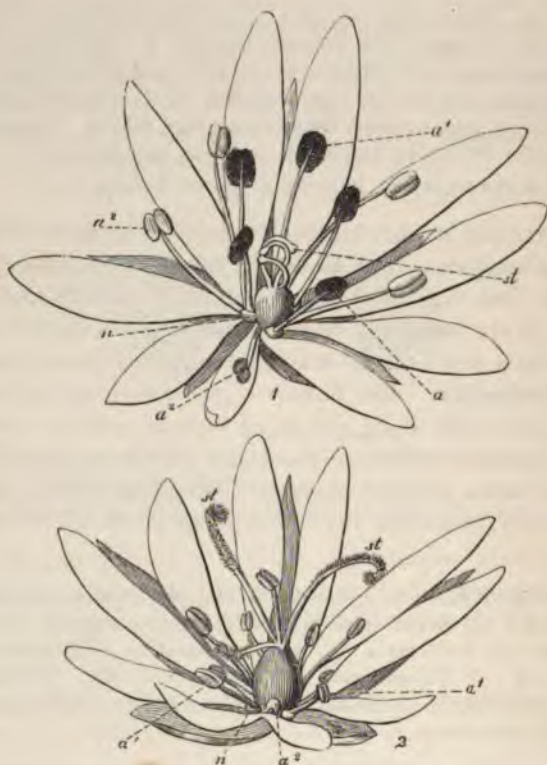


FIG. 42.—*Stellaria graminea*, L.

- 1.—Flower in first stage. The five outer anthers are covered with pollen, and are bent inwards.  
 2.—Flower in last stage. All the anthers are empty and shrivelled. The styles are spread out above the stamens, and are recurved, turning their papillar surface upwards.  
 a', outer whorl of anthers; a'', inner whorl; n, nectary.

stigmatic papillæ in older ones. In default of insect-visits, the stigmas as they continue to curve outwards come in contact with the pollen-covered anthers. Insect-visits are scarce, as the inconspicuousness of the flowers would lead us to expect. I have only once found *Volucella bombylans*, L. (*Syrphidæ*), sucking honey on the flowers.

65. *STELLARIA HOLOSTEA*, L.—The arrangement of the flower resembles that of *S. graminea*; but the flowers are larger and more conspicuous, the nectaries are yellow, confined to the outer side of the outer stamens, provided above with a honey-secreting pit, and yielding more abundant honey. The three stages are more clearly marked off than in *S. graminea*. In the first stage the outer stamens, in the second the inner ones, stand close round the centre of the flower, turning their pollen-covered surfaces more or less upwards,—the other five being in each case bent out of the way. In the first period the stigmas are bent inwards (as in 1, Fig. 42), in the second they stand erect but with their papillar sides turned inwards towards each other, in the third they are spread out (as in 2, Fig. 42), while the anthers have mostly fallen off or remain as withered scales attached to the corolla.

In flowers which I kept in my room however, self-fertilisation often took place, for the ends of the stigmas, as they spread outwards, often came in contact with the inner anthers still bearing their pollen, and moreover pollen often fell upon other parts of the stigmas.

Visitors : A. Diptera—(a) *Empidæ* : (1) *Empis tessellata*, F. ; (2) *E. opaca*, F., both frequent, s. ; (b) *Syrphidæ* : (3) *Rhingia rostrata*, L., ab., s. and f.p., standing on a petal and applying the proboscis now to the base of the flower, now to the anthers ; (4) *Eristalis arbustorum*, L., s. and f.p. ; (5) *Platycheirus peltatus*, Mgn., do. ; (6) *Syrphus ribesii*, L., do., ab. ; (c) *Muscidæ* : (7) *Hydrotaea dentipes*, F., s. B. Hymenoptera—(a) *Apidæ* : (8) *Apis mellifica*, L. ♀, ab. and persistent, s. (May 27, 1871) ; (9) *Nomada flavoguttata*, K. ♀ ; (10) *N. ruficornis*, L. ♀ ; (11) *Andrena cineraria*, L. ♀ ; (12) *A. parvula*, K. ♀, the last four s. ; (13) *Halictus cylindricus*, F. ♀, f.p. ; (b) *Tenthredinidæ* : (14) *Cephus pallipes*, Kl., s. C. Coleoptera—(a) *Nitidulidæ* : (15) *Meligethes*, ab., s. ; (b) *Edemeridæ* : (16) *Edemera virescens*, L. (Tekl. B.) D. Lepidoptera—*Rhopalocera* : (17) *Pieris napi*, L., s. E. Thysanoptera—(18) Thrips, ab. See also No. 590, II.

66. *STELLARIA MEDIA*, Vill.—The flowers are less conspicuous than the two preceding species, and, since they appear at all times of the year except in severe frost, they are for a great period shut out from insect-visits ; they therefore depend largely on self-fertilisation. Accordingly they differ considerably in their arrangement from the former species. Of the ten stamens, there are almost always some, usually five to seven, abortive ; and, on the whole, I think that the number of abortive stamens is greater the colder the time of year. The five inner stamens are always reduced, and often disappear completely ; the five outer ones, which bear the

honey-glands on the outer side of their bases, only show signs of abortion when the inner series are all abortive; at most, two of them disappear, but the corresponding glands always remain.

In sunny weather so much honey is secreted that the five drops are easily seen by the naked eye. The stamens, especially when their number has been reduced to three, come to maturity in slow succession. Immediately after the flower opens, the first anther begins to dehisce, and the stigmas still stand erect with their papillar sides turned inwards; but their tips are already slightly outspread. While the second and third stamens dehisce, the stigmas expand fully, and turn the whole of their papillar surfaces upwards. So from the beginning cross-fertilisation and self-fertilisation, in the event of insect-visits, are both equally likely; in absence of insects the stigmas regularly fertilise themselves by coming in contact with the anthers. This self-fertilisation is undoubtedly efficient, for *S. media* produces abundant seed in winter when no insects are about, and in long-continued rainy weather.

*Stellaria media* has the greatest chance of cross-fertilisation in early spring, for before that time no insects are on the wing, and afterwards many more attractive flowers compete with it. My own observations confirm this.

A. Hymenoptera—*Apidae*: (1) *Andrena Gwynana*, K. ♀, s. and c.p. (April 11, 1869); (2) *A. albicans*, K. ♂, s. (do.); (3) *A. dorsata*, K. ♀, s. (do.); (4) *A. parvula*, K. ♂, s. (April 21, 1869); (5) *A. albicus*, K. ♂, s. (do.); (6) *Osmia rufa*, L. ♂, s. (April 17, 1869). B. Diptera—(a) *Syrphidae*: (7) *Syritta pipiens*, L., s. (May 27, 1870); (b) *Muscidae*: (8) *Chlorops circumdata*, Mgn., diligently s. (March 9, 1872); (9) *Musca corvina*, F., do.; (10) *M. domestica*, L., do. C. Thysanoptera—(11) Thrips, dusted with pollen, creeping in and out of the flower (April 30, 1868). See also No. 590, II.

*Stellaria cerastoides*, L., is homogamous and is visited by Diptera. It fertilises itself in case of need (609).

67. *ARENARIA (M€HRINGIA) TRINERVIA*, L.—At the base of the expanded flower, on the outer side of the base of each outer stamen, we see a rather large drop of honey. The fleshy swellings at the bases of these stamens, which act as honey-glands, are so strongly developed and extend so far on either side, that they coalesce, and the five together form a ring round the ovary; from this ring the five inner stamens (which alternate with the others, and stand opposite to the petals) seem to spring.

When the flower opens, the stigmas are already separated and turn their rough papillar surface upwards, while the anthers remain

closed. In the second stage, the anthers of the outer and longer stamens dehisce; in the third stage those of the inner and shorter stamens, the stigmas still remaining fresh. The flowers are thus proterogynous with long-lived stigmas. Cross-fertilisation is likely to occur not only in the first stage, but also in the later stages, since an insect on alighting will probably touch the stigmas before the stamens.

In several cases I have found the outer stamens so much aborted as to be scarcely half the length of the inner series, and bearing tiny shrunken anthers devoid of pollen. Here apparently the time between the ripening of the stigmas and that of the stamens was lengthened, and hence the chance of cross-fertilisation increased. In default of insect-visits, self-fertilisation is attained by the stamens (both outer and inner) bending inwards, still covered with pollen, and coming in close contact with the stigmas.

I found a small beetle, *Olibris affinis*, Sturm, one of the *Phalacridæ*, licking honey on this flower.

*Arenaria (Mæhringia) muscosa*, L., is fertilised by *Syrphidæ* (609).

*Honkeneya (Ammodenia) peplodes*, Ehrh., is polygamous (Warm-ing, 762).

*Sagina nodosa*, E. Meyer, is proterandrous (17, 38) and visited by *Anthrax* (609).

The following additional species are discussed in my *Alpenblumen*:—*Arenaria biflora*, L.; *Alsine recurva*, Whlbn.; *A. verna*, Bartling; *Cherleria sedoides*, L.; *Cerastium alpinum*, L., *C. latifolium*, L.

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#### REVIEW OF THE ALSINÆÆ.

The foregoing *Alsinææ* are all more or less dichogamous, and are mostly proterandrous in various degrees, *Arenaria Trinervia* being proterogynous. Dichogamy is the more marked the more conspicuous the flowers, and the more abundant the visits of insects. Self-fertilisation is totally excluded in none of the above-mentioned forms, and is the better insured, the more inconspicuous the flowers are, and the more scanty the insect-visits either from that cause or on account of the unfavourable time of year. The insect-visitors are very various, on account of the accessible position of the honey, but consist chiefly of flies and the less specialised bees.

Most of the above remarks hold good also for the species which

I have observed on the Alps. *Alsine verna*, Jacq., *Cherleria sedoides*, L., and *Mehringia muscosa*, L., are so markedly proterandrous, that spontaneous self-fertilisation can only rarely and exceptionally take place in them. *Arenaria biflora*, L., and *Cerastium latifolium*, L., also ripen their anthers before their stigmas, but, in default of insect-visits, fertilise themselves.

I found *Stellaria cerastoides*, L., to be homogamous, in which respect it stands alone among the higher Alpine Alsineæ.

As bees are scarce in the higher regions of the Alps, Diptera take their place as cross-fertilisers of the Alsineæ more than in the lower grounds, and were alone observed on several of the above-mentioned species (609).

Dr. T. Ludwig of Greiz has recently made the interesting discovery that most if not all of the distinctly proterandrous Alsineæ are also gynodioecious; and that the plants with small and purely pistillate flowers are chiefly in bloom at the beginning of the flowering-period of the large-flowered hermaphrodite plants. So these subsidiary pistillate plants make up for the preponderance of the staminate condition in the hermaphrodite flowers at that time (426, 427).

#### ORD. CARYOPHYLLÆ; c. POLYCARPÆ.

*Polycarpon tetraphyllum*, L., has cleistogamic flowers (Batalin, 40).

#### REVIEW OF THE CARYOPHYLLÆ.

The *Caryophyllæ* exhibit an interesting series of gradations in the concealment of their honey, while the anthers remain throughout fully exposed; a comparison of their insect-visitors will thus show what effect differences in the situation of the honey produce.

The flowers of *Alsineæ*, and the short and wide flowers of *Gypsophila paniculata*, which all expose their honey freely, are chiefly frequented by flies and by a few beetles and other short-lipped insects; when visited by bees, it is either by the least specialised forms (*Proscopis*, *Halictus*, *Andrena*) or by the most specialised and most diligent (*Apis*). *Lychnis flos-cuculi*, whose honey is hidden 9 to 10 mm. deep, and beyond the reach of short-lipped insects, is almost exclusively visited by highly specialised

bees and by Lepidoptera, one drone-fly, *Rhingia*, coming also to share the honey. The benefit which results from and has brought about the lengthening of the tube in *Lychnis flos-cuculi* lies in the fact that, by excluding short-lipped insects from the honey, a larger number of insects with long proboscides are tempted to come, and these, requiring more food, are more diligent in their visits and in their work as cross-fertilisers. That the exerted anthers can be robbed by pollen-eating flies and pollen-collecting bees is scarcely a disadvantage; for the pollen is seldom completely removed, and these pollen-seeking insects act as subordinate fertilisers.

When the passage to the honey is still further lengthened and narrowed, as in the species of *Dianthus*, *Saponaria*, and *Lychnis*, even bees are excluded and Lepidoptera only can gain access. For this result to be advantageous we must suppose that the visits of Lepidoptera are the better insured by exclusion of other insects. Exposure of the anthers is as little injurious here as in *Lychnis flos-cuculi*. As the honey gets more deeply concealed, and access more strictly limited to butterflies, we find *pari passu* among the *Caryophyllææ* increasing development of sweet scents, bright red colours, fine markings round the entrance of the flower, and indentations at the circumference. All these characters, which are so attractive to us, seem to have been produced by the similar tastes of butterflies.

#### ORD. HYPERICACEÆ.

68. *HYPERICUM PERFORATUM*, L.—The flowers, from their size and bright colour, and from numerous plants being usually associated together, are very conspicuous, and attract many insects seeking both honey and pollen; they however contain no honey, and possess no contrivances to insure cross-fertilisation. The large production of pollen, and the capability for self-fertilisation compensate in part for these disadvantages. The numerous stamens, usually over eighty in number, radiate from the bottom of the flower in three groups, which are united at the base; the anthers are directed upwards and dehisce in rather quick centrifugal succession, covering themselves with pollen. The three styles also radiate outwards, so that their terminal stigmas, which are developed simultaneously with the anthers, come to stand on a level with the anthers in the intervals between the groups of stamens. Since these staminal bundles usually touch one another, and sometimes interlock slightly at their

them increase the chance of cross-fertilisation; rendering it likely in spite of the great number of anthers, that an insect on alighting will touch a stigma first, though self-fertilisation is also very probable. In all, self-fertilisation occurs in default of insect-visits, and is without doubt the usual mode of reproduction in the less conspicuous forms.

*Cratogeomys formosus* has dimorphic flowers (167, 213).

#### ORD. MARCGRAVIACEÆ.

In this order bracts secrete honey and make the flower conspicuous by their bright colours. They have accordingly the most various forms (spurs, spathes, etc.), and are of as much importance to the plant as petals usually are. Delpino bases a new subdivision of the order upon the modifications of the bracts. The flowers are protogynous.

In *Marcgravia nepenthoides* there occurs beneath a wreath of pendulous flowers a group of honey-secreting cups. They attract insects, which in turn attract insectivorous birds, and these, while feeding on the insects sitting upon the nectar-cups, touch and cross-fertilise the flowers above (56).

An interesting paper on Marcgraviaceæ and their Nectaries, with fine figures, was contributed by Ludwig Wittmack to *Kosmos*, vol. v., 1879 (784.)

#### ORD. MALVACEÆ.

*MALVA SILVESTRIS*, L., and *M. ROTUNDIFOLIA*, L.—These species often occur together, and flower side by side for months at a time. In the struggle for existence, *M. rotundifolia* has the advantage in being content with poorer soil, in the appearance of its flowers from one to several weeks earlier, and in the possibility of regular self-fertilisation; *M. silvestris*, on the other hand, in its more vigorous growth, and much greater attractions for insects. These advantages seem to balance one another, for, about Lippstadt at least, both species grow together in equal abundance.

In both species, a pyramidal group of anthers occupies the middle of the young flower, and surrounds the stigmas which are still unripe and folded together; later on, the stigmas become exerted and radiate outwards. Honey is secreted in five pits between the bases of the petals, and protected by hairs, and insects

seeking it must wipe off pollen from the anthers in young flowers and apply it to the stigmas in older ones. In *Malva silvestris*, which attracts insects by the larger size and brighter colour of its flowers, and receives very numerous visits, the ends of the filaments, before the stigmas are mature, curl outwards so far that spontaneous self-fertilisation is impossible. *M. rotundifolia*, whose much smaller and paler flowers attract few insects, regularly fertilises itself in default of insect-visits, for its anthers remain extended in such a position as to be touched by the papillate sides of the curling stigmas. (Fig. 44, 5).

The following lists of insects which I have observed during four summers upon the two forms, show how great is the difference in this respect between them.



FIG. 44.

1—4.—*Malva silvestris*. 1, essential organs from a bud; 2, ditto, in the first stage of the flower; 3, ditto, between the first and second stages; 4, ditto, in the second stage.  
5.—*Malva rotundifolia* in the act of self-fertilisation.

#### 69. MALVA SILVESTRIS, L. :—

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, s., very ab.; (2) *Bombus lapidarius*, L. ♀, ab.; (3) *B. hortorum*, L. ♀; (4) *B. silvarum*, L. ♀; (5) *B. agrorum*, F. ♀; (6) *Cilissa hæmorrhoidalis*, F. ♀ ♂, freq.; (7) *Andrena parvula*, K. ♂; (8) *A. Gwynana*, K. ♀; (9) *A. fulvicrus*, K. ♀; (10) *Halictus maculatus*, Sm. ♀; (11) *H. albipes*, F. ♀; (12) *H. morio*, F. ♀; (13) *H. Smeathmanellus*, K. ♀; (14) *H. zonulus*, Sm. ♂; (15) *Nomada lateralis*, Pz. ♀; (16) *Osmia ænea*, L. ♂; (17) *Megachile Willughbiella*, K. ♂; (18) *M. ligniseca*, K. ♂; (19) *Cœlioxys simplex*, Nyl. ♀ ♂; (20) *Chelostoma campanularum*, L. ♂,—all these twenty species though always dusted with pollen, never collected it, but came for honey only; (21) *Ch. nigricorne*, Nyl. ♂ ♀, very ab., both s. and ep., this is the only species which I have seen collecting the pollen; (22) *Prosopis hyalinata*, Sm. ♂; (23) *P. communis*, Nyl. ♂ ♀, freq.; (24) *P. signata*, Schenck, ♂; (25) *P. pictipes*, Nyl. ♂; (26) *P. dilatata*, K. ♂, all sucking; (b) *Ichneumonidae*: (27) various species,—I am unable to say whether they succeeded in reaching the honey. B. Diptera—(a) *Stratiomyida*: (28) *Sargus cuprarius*, L. (s. seemed to derive no advantage

from the flowers, though attracted by them ; (b) *Syrphidæ* : (29) *Rhingia rostrata*, L., s., ab. C. Lepidoptera—(30) *Pieris rapæ*, L., s. D. Coleoptera—(31) *Haltica fuscicornis*, L., in the flowers. See also No. 590, II.

#### 70. *MALVA ROTUNDIFOLIA*, L. :—

Visitors : Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀ ; (2) *Bombus agrorum*, F. ♀ ; (3) *Anthophora quadrimaculata*, F. ♂ ; (4) *Halictus morio*, F. ♂, all sucking. See also No. 590, II.

The following observation shows that even *Malva silvestris* is not perfectly adapted to its conditions of life. In the afternoon, when the flowers begin to close, I have very often seen hive-bees clambering up the outside of the calyx of closed but still fresh flowers ; thrusting the proboscis past the sepals, they emptied the nectaries from outside. Sometimes I have even seen bees, after sucking several closed flowers in this manner, perform the same operation on the next open flower. Thus the flowers of *Malva silvestris* have not sufficiently secured their honey from plunder.

71. *MALVA ALCEA*, L.—The flowers standing on longer stalks, and expanding their rosy petals to a diameter of 40 mm., are still more conspicuous than those of *M. silvestris*. Self-fertilisation is obviated by the same arrangement as in *M. silvestris*, and insect-visits are probably at least equally numerous. I have only once, in scarcely favourable weather, observed a few specimens in flower (July 13, 1868).

Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, very ab., s., covering itself with pollen ; (2) *Cilissa hæmorrhoidalis*, F. ♀, s. ; (3) *Halictus cylindricus*, F. ♀, s. See also No. 590, II.

72. *MALVA MOSCHATA*, L.—The flowers are as distinctly proterandrous as those of the three foregoing species. According to a sketch which I made in 1867, the ends of the filaments curve downwards on the withering of the anthers ; the stigmas spread out above them, apparently obviating self-fertilisation. However, at that time I did not pay particular attention to cases where self-fertilisation occurs in default of insect-visits.

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. ; (2) *Cheilosoma nigricorne*, L. ♀, s. ; (3) *Andrena Coitana*, K. ♂, s. (Sld.). B. Diptera *Bombylidæ* : (4) *Systoechus sulfureus*, Mikan s. (Sld.). C. Lepidoptera : (5) *Hesperia silvanus*, Esp., s.

Delpino mentions *Xylocopa violacea* as a visitor of the *Malvaceæ* (172). Dr. Ogle says (631) that in many *Malvaceæ* anthers

and stigmas ripen together, and self-fertilisation takes place regularly; he says that in these forms no nectaries are present, since the aid of insects is not required. Unfortunately he does not name the species to which he refers.

*Anoda hastata*, Cav.—Hildebrand figures and describes the proterandrous flowers. In the first stage the ripe anthers are erect and the stigmas are folded down, while in the second the stigmas project above the anthers (351).

*Gossypium herbaceum*, L., has floral and extra-floral nectaries. It is visited by Ruby-throated Humming-birds, and by numerous insects (730).

*Abutilon*, Gärtn.—My brother Fritz Müller has performed many experiments on this plant at Itajahy, with the following results:—

(1) All the species of *Abutilon* growing there, and their hybrids, are barren (with perhaps one exception) when fertilised with their own pollen.

(2) In those species which are unproductive with their own pollen, the pollen of their near relations (the parent-plants or their offspring) is less efficient than pollen from more distantly related or unconnected plants.

(3) The application of pollen from several different species gives a greater yield of seed than pollen from a single other species only.

(4) The simultaneous application of pollen of two species always produces seedlings of two kinds: not as in the experiments of Koelreuter and Gärtner on other plants, where the simultaneous application of two species of pollen always produced seedlings of one kind only.

(5) Among hybrids of the genus *Abutilon*, there is more or less complete sterility between nearly related individuals—between parent-plants and their offspring, between offspring of the same parents, or even between plants which have only one parent in common.

By considering from a common point of view the diminution of fertility in too close interbreeding and in the production of hybrids, Fritz Müller arrives at the following law:—Every plant, to produce vigorous and prolific offspring, requires a certain degree of difference between the male and female principles which coalesce; and when this amount of difference is too great or too small, *i.e.* when the parent-plants are too distantly or too closely related, the productiveness falls off. Further, the greater

75. *LINUM USITATISSIMUM*, L.—This flower resembles the preceding one in regard to its honey, and to the simultaneous ripening and relative positions of anthers and stigmas; hence also in the likelihood of cross-fertilisation in case of insect-visits, and in the constancy of self-fertilisation if they fail.

Hildebrand has shown by direct experiment that self-fertilisation is efficient.

The flowers are more conspicuous and therefore more visited by insects than those of *L. catharticum*. Sprengel observed a humble-bee on them; I have noted:—

A. Hymenoptera—*Apida*: (1) *Apis mellifica*, L. ♀, ab., s.; (2) *Halictus cylindricus*, F. ♀, c.p. B. Lepidoptera—*Noctua*: (3) *Plusia gamma*, L., s. See also No. 590, II.

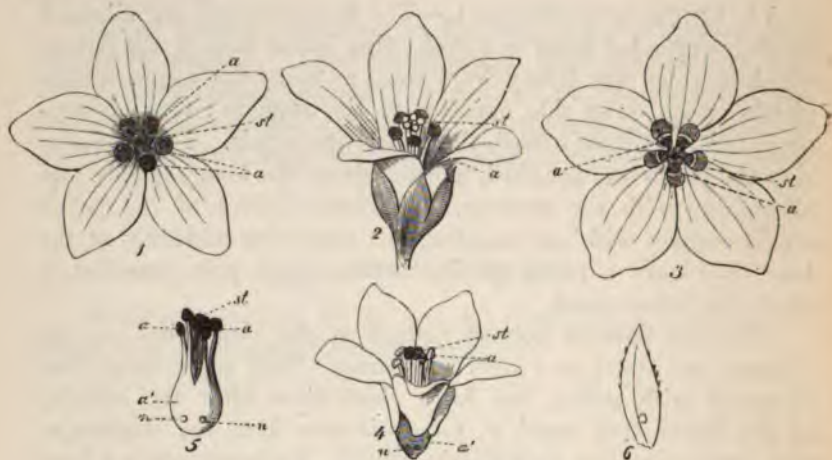


FIG. 45.—*Linum catharticum*, L.

- 1.—Young flower, from above; the anthers are not yet in contact with the stigmas.
  - 2.—Ditto, viewed obliquely from above.
  - 3.—A slightly older flower, from above; the five anthers are covered with pollen, and are in contact with the stigmas.
  - 4.—Flower after removal of the calyx, to show the insertion of the petals and the position of the nectaries.
  - 5.—Essential organs removed from the flower, in the position of self-fertilisation.
  - 6.—Sepal from the inside, with a drop of honey.
- a, anther; st, stigma; n, nectary; a', coherent filaments.

The dimorphic species of *Linum* have been the subject of several important researches.

Darwin, as early as 1863, recorded dimorphism in *L. grandiflorum*, Desf., *L. perenne*, L., and *L. flavum*, L., and made experiments on the two first. In *Linum grandiflorum* the short-styled flowers gave, on self-fertilisation, more seed than the long-styled, which remained almost barren. Both proved to be far

more fertile when legitimately fertilised. As a rule the pollen-grain failed to develop its pollen-tube when on the stigma of a flower of its own kind (157).

In *Linum perenne* illegitimate pollination of the long-styled form was quite unproductive, and in the short-styled form very nearly so; in both forms, legitimate pollination led to full fertility in three cases out of four. Hildebrand found that in this species short-styled flowers were quite infertile with their own pollen, with that from another flower on the same plant, or from any other short-styled flower; but invariably fertile to pollen from a long-styled flower (339, 340).

In *Linum Lewisii*, Pursh. (*L. Sibiricum*, D.C.), according to Planchon, each plant bears flowers of three kinds, one long-styled, one short-styled, and one with styles and stamens of equal length; that is to say, it is *trimorphic*, though not in the same sense that *Lythrum Salicaria* is so. Dr. Friedrich Alefeld enumerates twenty-nine dimorphic species of *Linum*, all natives of Europe, Asia, or North Africa; while all the species from North and South America and from the Cape are monomorphic (1). (Cf. Darwin, 167.)

*Radiola linoïdes*, D.C. (*R. millegrana*, Sm.), is visited by minute Diptera (590, II).

*Erythrozyton* is dimorphic.

#### ORD. MALPIGHIACEÆ.

*Camarea*, St. Hil., and *Janusia*, A. Juss., according to Adr. de Jussieu, have cleistogamic as well as normal flowers; *Aspicarpa ureus*, Rich., occurs with only cleistogamic flowers (531); *Gaudichaudia*, H. B. and K., also is placed among cleistogamic forms by Kühn (399).

In *Bunchosia gaudichaudiana* the glands on the exterior of the calyx seem not to be protective in function. They are visited by various bees (*Tetrapedia* and *Epicharis*), which in feeding on them dust the under surface of their bodies with pollen, with which they cross-fertilise other flowers (360).

#### ORD. GERANIACEÆ.

##### Tribe Geranieæ.

76. GERANIUM PALUSTRE, L.—The structure of this flower was thoroughly described and figured by Sprengel, who, however, observed no insect-visitors. In sunshine the flowers expand their

purple petals to a diameter of 30 to 40 mm., and turn towards the sun, so that, being brightly illuminated, they are visible at a great distance.

The darker lines which converge to the centre, and the pale-coloured claws of the petals, serve to direct insects towards the honey, which is secreted by five glands at the bases of the outer stamens, and protected from rain by hairs at the bases of the petals; it is accessible to very short-lipped insects. Insect-visits are so frequent that the power of self-fertilisation has become completely lost. Each flower passes through three well-marked stages, in which first the five outer stamens, next the five inner stamens, and thirdly, when these have withered, the five stigmas, become in turn ripe and stand up prominently in the middle of the flower. Each whorl of stamens bends outwards as its anthers wither.

Near Lippstadt this plant is confined to a single locality, and I have only once watched it, for about half an hour, in a light east wind and changeable sky (August 21, 1871). I was convinced in this short time of the great number of insects which frequent the plant. Whenever the sun shone out, I found the flowers visited by numerous flies and bees, especially species of *Halictus*.

A. Hymenoptera—*Apidae*: (1) *Halictus cylindricus*, F. ♂; (2) *H. albipes*, F. ♂; (3) *H. flavipes*, F. ♂; (4) *H. longulus*, Sm. ♀; (5) *H. nitidiusculus*, K. ♀ ♂; (6) *H. zonulus*, Sm. ♂; (7) *Andrena dorsata*, K. ♂; (8) *A. fulvicrus*, K. ♂; (9) *Prosopis communis*, Nyl. ♀. B. Diptera—(a) *Syrphidae*: (10) *Rhingia rostrata*, L.; (11) *Melithreptus scriptus*, L.; (12) *Eristalis tenax*, L.; (13) *Helophilus pendulus*, L.; (14) *Platycheirus peltatus*, Mgn.; (b) *Muscidae*: (15) small species of *Anthomyia*. C. Lepidoptera—(16) *Pieris rapæ*, L.,—all sucking.

77. *GERANIUM PRATENSE*, L.—This is generally the most conspicuous and most abundantly visited plant in the meadows where it grows, just as *G. palustre* is in the marshes. It agrees in structure for the most part with the former species, and like it has lost the power of self-fertilisation. Hildebrand gives (351, p. 19) a drawing and short description of its markedly proterandrous flowers. He has shown that, at the time when the anthers dehisce and are bent over the stigmas, these latter as a rule are incapable of fertilisation; they become capable of fertilisation when the anthers have diverged away from them, and finally lose this capability on the falling off of the petals (342.)

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, very ab., s.; *Osmia rufa*, L. ♀, s. (May 27, 1868); (3) *Chelostoma nigricorne*, L. ♀, s.

(Thur.) ; (4) *Stelis aterrima*, Pz. ♀ ♂ (Thur.), s. ; (5) *Andrena Coitana*, K. ♂ (Sld.), ♀ (Thur.), s. ; (6) *Halictus cylindricus*, F. ♂ ; (7) *H. albipes*, F. ♂ ; (8) *H. leucozonius*, K. ♀ ; (9) *H. longulus*, Sm. ♂ ; (10) *H. maculatus*, Sm. ♂ (Thur.)—all sucking ; (11) *H. lucidulus*, Schenck, ♀, c.p. ; (12) *Prosopis hyalinata*, Sm. ♂, s. B. Diptera—*Syrphidæ*: (13) *Melithreptus pictus*, Mgn., f.p. See also No. 590, II.

78. *GERANIUM PYRENAICUM*, L.—The flowers are proterandrous, and regularly fertilise themselves in default of insect-visits. Before the bud expands, all the filaments have their thin ends bent slightly outwards.

As soon as the flower opens, the five outer stamens, which alternate with the petals and which bear at their base the honey-glands, rise up so that their anthers overtop the divisions of

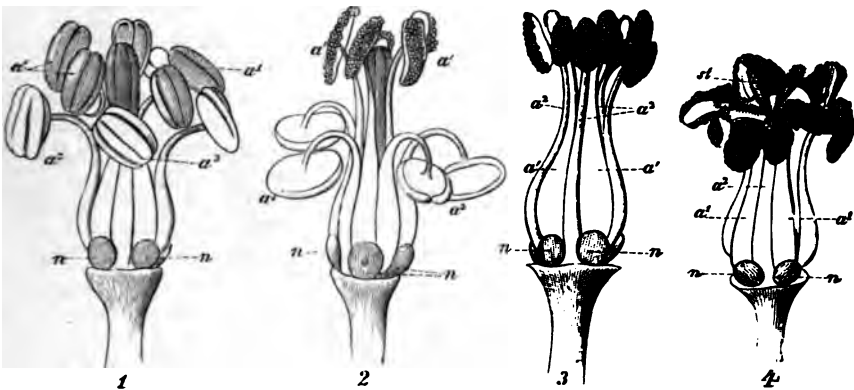


FIG. 46.—*Geranium pyrenaicum*, L.

1-4.—Positions of the reproductive organs at successive stages.

the stigma, which are still closely united, and each anther turns that side where dehiscence is about to take place outwards and upwards: this whole surface becomes covered with pollen. At the same time the thin ends of the five inner stamens curve downwards, so that their anthers which are still closed are out of the way of insects, and do not hinder them from dusting themselves with pollen. A day later these five inner stamens rise up and dehisce, so that now the stigmas are surrounded by a circle of ten anthers, all dusted on their outer sides with pollen.

After a day or two more, the stigmas at last begin to separate from one another, and when they do so, they lie on a level with the anthers. If the pollen has not in the meanwhile been removed, an insect-visitor may now accomplish self-fertilisation as easily as

cross-fertilisation, but if insect-visits have taken place to a sufficient extent, the pollen is wholly removed before the stigmas separate, and cross-fertilisation is the inevitable result of further insect-visits. If insects do not visit the flower at all, self-fertilisation always takes place, as the edges, at least, of the recurving stigmas come in contact with the pollen, as I have repeatedly seen in the case of specimens flowering in my room.

The fertilisation of the plant is therefore provided for under all possible conditions.

I have not had a direct opportunity of observing this plant fertilised by insects; but in sunny weather its insect-visitors must be fairly numerous, for Herr Borgstette, to whom I am indebted also for living examples of the plant, sent me the following insects caught by him on its flowers at Teklenburg:—

A. Hymenoptera—(a) *Apidae*: (1) *Andrena fulvago*, Christ. ♀, with pollen of *Geranium* on its collecting-hairs; (2) *A. Gwynana*, K. ♀ ♂; (3) *A. parvula*, K. ♀; (4) *A. dorsata*, K. ♀; (5) *Halictus cylindricus*, F. ♀; (6) *H. maculatus*, Sm. ♀; (7) *H. Smeathmanellus*, K. ♀; (8) *Sphecodes gibbus*, L. ♀; (9) *Osmia fusca*, Christ. (bicolor, Schrank), ♀; (10) *Chelostoma nigricorne*, L. ♀; (b) *Sphegidae*: (11) *Ammophila sabulosa*, L.; (c) *Vespidae*: (12) *Odynerus* (*Hoplopus*) *quinquefasciatus*, F. B. Diptera—(a) *Syrphidae*: (13) *Helophilus floreus*, L.; (14) *Chrysotoxum bicinctum*, L.; (15) *Melithreptus taeniatus*, Mgn.; (16) *M. pictus*, Mgn.; (17) *Syrphus balteatus*, Deg.; (18) *S. ribesii*, L.; (19) *S. pyrastrii*, L.; (20) *Ascia podagrica*, F.; (21) *Rhingia rostrata*, L.; (22) *Pelecotoma tricineta*, Mgn.; (b) *Muscidae*: (23) *Echinomyia fera*, L.; (24) *Scatophaga stercoraria*, L. C. Coleoptera—(a) *Dermestidae*: (25) *Byturus funatus*, L.; (b) *Cistelidae*: (26) *Cistela murina*, L.; (c) *Malacodermata*: (27) *Malachius aeneus*, L.

On the Alps I found *G. pyrenaicum* abundantly visited by insects, and incapable of spontaneous self-fertilisation (609). The stamens bent far outwards before their anthers withered, and the stigmas did not expand until all the anthers or at least the outer five had fallen off.

79. *GERANIUM SANGUINEUM*, L., in spite of its flowers being much more conspicuous, agrees fully in the manner of its fertilisation with *G. pyrenaicum*; its conspicuousness seems therefore not to insure cross-fertilisation in any greater degree but only to compensate for its more shady habitat.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Halictus maculatus*, Sm. ♀; (2) *H. sexnotatus*, K. ♀ (both usually alight on a petal, and go round the flower, licking one nectary after another—their sides rub against the anthers in young flowers and the stigmas in old ones,—sometimes they alight

in the middle of the flower) ; (b) *Sphegidae* : (3) *Oxybelus* sp., s. B. Diptera—*Syrphidae* : (4) *Rhingia rostrata*, L., settles sometimes in the middle of the flower, sometimes on a petal, and sucks all the five drops of honey in succession. See also No. 590, II., and No. 609.

80. *GERANIUM MOLLE*, L.—When the flower opens, the divisions of the stigma lie close together so that their papillar sides are hidden. The anthers are all closed and distant from the middle of the flower; the thin ends of their filaments are bent outwards, the inner row of stamens which stand opposite to the petals being bent farther outwards than the others which alternate with the petals.

Now the outer stamens begin, one after the other, to bend inwards, so as to lie over the apex of the stigma, and to dehisce there; the flower is thus for a time male only. But even before the first five stamens have all dehisced, the divisions of the stigma begin to separate; so that the five anthers which lay over their

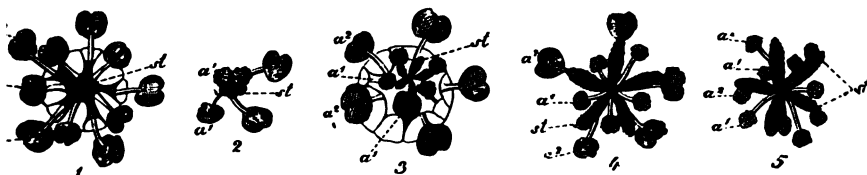


FIG. 47.—*Geranium molle*, L.

1—5.—Reproductive organs in successive stages. In 2, the inner whorl of stamens has been removed.  $a'$ , outer stamens, alternating with the petals, and provided at the base with nectaries;  $a''$ , inner whorl, opposite the petals, bent further out than the outer whorl when the flower opens;  $st$ , stigma.

apices come to lie in the angles between them, and let some part of their pollen fall upon the stigmatic papillæ.

While the divisions of the stigma are expanding still more widely, the inner anthers, which hitherto were closed, begin to curve inwards and to dehisce. When all the anthers have shed their pollen, they lie partly in the angles, partly over the ends of the outspread stigmas, and only a little above them; so that insects which alight in the middle of the flower touch anthers and stigmas at the same time, and can accomplish self-fertilisation as well as cross-fertilisation.

The likelihood of self-fertilisation is thus greater in these less conspicuous and therefore less visited flowers than in either of the two preceding species, since anthers and stigmas come into immediate contact with one another early in the flowering period. The probability of cross-fertilisation is in consequence so much the

the flower, even with the most minute insect, the possibility of self-fertilization remains throughout.

*Notes.*—(1) *Spiza*.—(2) *Spizella*.—(3) *Arch. pelagica*, F. & C. very ab.; (4) *Chrysomitris*, L. & C.; (5) *Monticola*, L. & C.; (6) *Syrnistris*, L. & C.; (7) *Monticola*, L. & C.; (8) *Spizella*, L. & C. (I saw the first of these on June 30, 1871, in a spot where *G. molle* and *G. pusillum* were growing together, dip its tongue into one flower of *G. molle*, but alighted immediately for *Glechoma*.—I noticed this apparently trivial circumstance because it shows (1) that *G. molle* and *G. pusillum* were growing together, (2) that even *G. molle* has not sufficient attraction to win the services of the hive-bees. See also No. 599, II.

85. *GERANIUM PUSILLUM*, L.—Although on superficial examination very easily confused with *G. molle*, *G. pusillum* differs considerably from that species in the structure of its flower.

Only the five stamens which alternate with the petals bear anthers, and these stamens are provided at their base with honey



FIG. 48.—*Geranium pusillum*, L.

Essential organs of a flower which is just opening, seen from above: *a*, stigma; *st.*, anther.

glands. When the flower opens, the stamens are all erect and closely applied to the pistil. The five divisions of the stigma are spread out for half their length, their papillary surfaces are turned upwards, and the anthers, which are still closed, lie a little below the stigmas in the angles between them. The flower therefore is as yet female only, and can only be fertilised through insect agency by pollen from older flowers.

Soon after this the anthers dilate, covering themselves on both sides with viscid pollen-grains, and the stigma spreads further apart, so that the anthers come to lie in the angles between them and dust the papillae on their upper surface. It now is now as much male as female. The stigma is now covered with other pollen than with its own, and the flower has already begun to fertilise.

As long as the stigma is covered with other pollen than its own, while the style is still erect,

flower, so that the anthers, still dusted with pollen, are closely pressed together, and lie over the stigmas; they must therefore be touched before the stigmas by an insect alighting in the middle of the flower. In this stage the flowers are adapted for dusting the bellies of insect-visitors with pollen for the fertilisation of other flowers; but their own stigmas are more easily reached by their own than by other pollen.

The anthers now easily fall off, and one often finds the older flowers without anthers, but with five fully outspread stigmas. These flowers are therefore again female only, but their stigmas have already come in contact with their own pollen, though they may still be fruitful with that from younger flowers.

If we compare the flowers of *G. pusillum* with those of its near ally *G. molle*, with which it grows in company, and blooms at the same time, we see that the former are smaller and paler, and are accordingly more rarely visited by insects. In each case, however, the regular occurrence of self-fertilisation compensates for the great uncertainty of cross-fertilisation; and further, the very early development of the stigmas enables the rare insect-visits to be made full use of when they do occur. Finally, the more rapid development of the flower permits the number of anthers to be reduced to one-half.

In spite of frequent watching, I have only noticed the flowers of *G. pusillum* to be visited by one insect, a small gnat, *Ascia podagrica*, F., but by that on several occasions. It settled in the middle of the flower and sucked honey from it. See also No. 590, II.

#### REVIEW OF THE PRECEDING SPECIES OF GERANIUM.

If we exclude *G. sanguineum*, which grows in more shady spots, and arrange the other species according to the size and conspicuousness of their flowers, we get a series as follows:

(1) *G. palustre* and *G. pratense*; (2) *G. pyrenaicum*; (3) *G. molle*;

(4) *G. pusillum*. Practically the same series if we arrange

these species according to the increasing chance of cross-ferti-

fication in case of insect-visits, so also if we take them

in order of the degree of self-fertilisation in

*G. pratense* and *G. palustre*, ordinary flowers,<sup>1</sup> while

in *G. pyrenaicum* and *G. sanguineum*, it is probable, and even probable, that

of *G. silvaticum*.

cross-fertilisation is thoroughly insured through the separation of the sexual products both in time and space; (2) in *G. pyrenaicum*, self-fertilisation never takes place in the earlier period, but it takes place regularly though not abundantly towards the end of the flowering period if insect-visits do not occur,—cross-fertilisation is insured, as in the two preceding species, if insect-visits occur early, but if they are delayed till the second stage they result more easily than in the other two species in self-fertilisation also; (3) in *G. molle*, even if insect-visits occur early and abundantly, self-fertilisation is not excluded; and it takes place to a greater extent than in the former species long before the flowering period ends, if insect-visits do not occur,—though self-fertilisation is at no time excluded, cross-fertilisation is favoured in case of insect-visits, by the position of the reproductive organs in both stages of the flower; (4) in *G. pusillum*, self-fertilisation takes place abundantly in every case before the end of flowering, but if insect-visits take place in time, the stigma, which is developed before the anthers, receives pollen from outside before self-fertilisation can take place, and when pollen of the same flower is afterwards applied to the stigma it is probably rendered useless by the “prepotency” of the other: if insect-visits are delayed till a later period, so that pollen from outside is brought only to a stigma already laden with pollen of its own flower, we may still suppose that the former outstrips the latter.

Thus in these *Geraniums* we see clearly how, as the number of insect-visits diminishes with the conspicuousness of the flower, the plant makes amends by an increasing likelihood of self-fertilisation for the diminished chance of cross-fertilisation.

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*Geranium dissectum*, L.—The manner of fertilisation is similar to that of *G. pusillum*, but the flower has ten anthers. When it opens, the stigmas already stand widely outspread, and the anthers which stand close around them are still closed and dehisce gradually one after another, dusting the stigmas with pollen. I have seen it visited by flies and by *Andrena* (vide No. 590, II. p. 217).

82. *GERANIUM ROBERTIANUM*, L.—When the flower opens, the five stigmas are folded close together; the five outer stamens stand close round them, in the middle of the flower, and their anthers, which project a little above the stigmas, dehisce, covering

their upper surfaces with pollen. The five inner stamens are still bent outwards as far as possible, so as to lie upon the petals and be out of the way of insects which alight on the flower. Before the period of the outer stamens is over, the stigmas separate and expand, so that their papillar surfaces which were hidden before are now fully exposed in the middle of the flower.

As the outer stamens wither, the five inner ones rise up to surround the style, which lengthens meanwhile, so that its five stigmas stand a little way above the circle of pollen-covered anthers.

Honey is secreted, as in all our *Geraniums*, by the outer side of the base of each outer stamen, and is collected in a slight hollow at the base of each sepal: it may be reached by means of a proboscis at least 7 mm. long, without which the insect must thrust its head into the narrow part of the flower. I have seen *Rhingia rostrata* in great abundance, sucking up the five honey-drops one after another with its proboscis, which is 11 to 12 mm. long; it stood first on one petal, then on another, and in older flowers its proboscis touched first the stigmas and then the ripe anthers, in younger ones the ripe anthers only. It effected cross-fertilisation regularly, but at times, in drawing out its proboscis, it must also have effected self-fertilisation. I have quite as often found this fly busy eating pollen. I have noted, in all, the following visitors:—

A. Diptera—*Syrphidæ*: (1) *Rhingia rostrata*, L., s. and f.p., ab. B. Coleoptera—(2) *Dasytes flavipes*, F., sucking and biting the petals. C. Lepidoptera—(3) *Pieris napi*, L., very ab., s. (Stromberg, May 15, 1868). See also No. 590, II.

Cross-fertilisation is here insured, at first by the early development of the outer stamens, and afterwards by the position of the mature stigmas above the level of the anthers; but self-fertilisation is not absolutely excluded. I have not included this species in the foregoing series, because I have not yet made sure whether self-fertilisation does result in default of insect-visits.

*Geranium silvaticum*, L., is not only widely distributed in Low Germany and in Britain, but occurs also in the Alps, where it extends to far above the limit of trees and is one of the most abundantly visited plants. I have found upon its flowers:—Coleoptera, 8; Diptera, 21; Hymenoptera, 24 (*Apidæ*, 17); Lepidoptera, 21: in all, 74 species.

This plant is historically interesting, since it suggested to Sprengel the first idea of his theory. It is also remarkable for being *gynodiæcious*, and for exhibiting transitions both towards

homogamy and towards dioecism (609). (List of visitors in Low Germany, 590 II. p. 218.

*Geranium phæum*, L., is proterandrous. The two whorls of stamens develop in succession, and the stigmas do not expand until the stamens have again bent outwards. The flowers are visited for their honey by humble-bees and by the hive-bee (229, 665).

*Geranium macrorhizon*, L., is proterandrous, and the earlier flowers are female only. The same is true of several species of *Pelargonium* (356, p. 479).

83. *ERODIUM CICUTARIUM*, L'Hérit.—The honey is secreted and stored as in all our other *Geraniums*; the five outer anthers

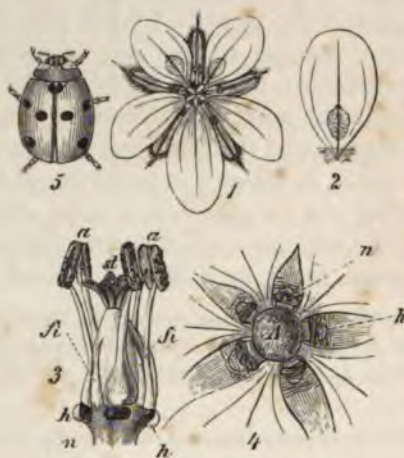


FIG. 49.—*Erodium cicutarium*, L'Hérit.

1.—Flower, seen from above and in front.

2.—One of the two superior petals, magnified half as much again, showing the hairs at its base which protect the nectar. The three dark lines converging towards the base form a "path-finder" common to all the petals; the elliptic spot is a "path-finder" peculiar to the two upper petals.

3.—The reproductive organs. *a*, anthers; *st*, stigma; *n*, nectary; *h*, drop of honey; *fi*, the five filaments of the inner whorl of stamens, whose anthers are aborted.

4.—Centre of the flower, after removal of the pistil. *A*, point of attachment of the pistil; *n*, nectaries, with their honey-drops protected by the two rows of hairs.

5.—*Coccinella septempunctata*, an awkward visitor of this flower.

only are fertile, as in *G. pusillum*. As in other *Geraniums* the flowers turn towards the sun, rendering themselves conspicuous, in spite of their short stalks, among all the other flowers of the bare, sunny slopes where they chiefly grow.

While in the species of *Geranium*, the flowers though set obliquely are quite regular, here there is a distinct difference

between the upper and lower petals, the (two, rarely three) upper ones bearing "path-finders" in the form of fine black lines, the (three, rarely two) lower ones being elongated to form convenient alighting-places.

The flowers are distinctly proterandrous, so that cross-fertilisation never fails if insect-visits take place in time: if they do not take place, then the flower is regularly self-fertilised.

I have only noted the following visitors:—

A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s. and c.p., ab. (Sprengel found hive-bees and humble-bees collecting pollen). B. Coleoptera—(2) *Coccinella septempunctata*, L., licking honey.

The awkward way in which this beetle, which is not fitted to feed on flowers, obtained the honey, was too amusing to pass by without notice. While seated on a petal, it applied its mouth to one of the nectaries at the base thereof; while so doing, the petal usually broke off, and the beetle was left clinging to the next petal, or fell with its own to the ground. In the former case it kept on its way round the flower, and frequently pulled off all five petals, one after another; but when it fell it was always at once on its legs again, running to another stalk of the same plant to climb up anew. I saw one beetle fall four times to the ground without growing wiser by experience.

Ludwig has published more comprehensive researches on the mechanism of fertilisation in *Erodium* (433, 434, 438).

#### Tribe *Pelargonice*.

Some general remarks on the structure of the flower in *Tropæolum* are given by Delpino (172); the structure in *T. majus*, L., was thoroughly described by Sprengel, who noted its proterandrous condition

#### Tribe *Oxalideæ*.

Hildebrand has investigated all the species of *Oxalis* in the Botanic Gardens of Berlin and Bonn, in the Royal Herbarium of Berlin, the Munich Herbarium, and the collections of Treviranus, A. Braun, and Selmeyer. He distinguishes twenty trimorphic species, whose different forms were in many cases looked upon as distinct species previously; fifty-one species possess two forms, and thirty have one only. Our three native species, *O. acetosella*, L., *O. stricta*, L., and *O. corniculata*, L., are shown to be monomorphic (348).

Experiments on artificial pollination and the growth of the resulting seeds, which Hildebrand afterwards instituted with two trimorphic species, *O. Valdiviana* and *O. Regnelli*, Miquel, led to results similar to those of Darwin in the case of *Lythrum Salicaria*. They showed (1) that productiveness is greatest, or exists only, after legitimate fertilisation; (2) that both parent-plants influence the form of the offspring; (3) that pollen-grains from stamens of equal length are of the same size, and diminish from the tallest to the shortest anthers.

Hildebrand gives a figure of the trimorphic flowers of *Oxalis gracilis*, Jacq. (348). H. v. Mohl has described the cleistogamic flowers of *O. acetosella* (531).

#### Tribe *Balsamineæ*.

*Impatiens Balsamina*, Tilo.—In younger flowers the anthers lie upon the still closed stigmas, and dust their pollen upon the backs of insects (bees) which dip their proboscides into the spur; in older flowers, when the crown of anthers has withered, the outspread stigmas come in contact with the same parts of the bee.

H. v. Mohl has described cleistogamic flowers in *Impatiens Noli-me-tangere*, L., and in North American species (531).

On cleistogamy in *Impatiens fulva*, Nutt, see M. A. Loche (417); on cleistogamy in both species, see Bennett (72, 79). *Impatiens parviflora*, D.C., according to Bennett, never produces cleistogamic flowers, but according to Henslow it is liable to spontaneous self-fertilisation.

North American species of *Impatiens* are visited by humming-birds (164).

#### ORD. *RUTACEÆ*.

84. *RUTA GRAVEOLENS*, L.—The most prominent features of the flower have been described by Sprengel.

A fleshy disc situated beneath the ovary secretes honey in eight to ten glands upon the bases of the stamens, sometimes in larger glands between these, besides producing small drops over its whole surface: the honey lies quite exposed and freely accessible. The strong scent and the greenish-yellow colour of the flowers seem able to attract only Hymenoptera and Diptera, the latter in very great numbers. The stamens, when the flower opens, lie two in each of the petals, which are hood-shaped and spread out horizontally. According to Sprengel, two stamens on opposite sides of the flower rise up simultaneously, bending inwards so that

their anthers now covered with pollen come to lie above the ovary in the middle of the flower; as they wither they bend back again, and two others take their place. The stigma only ripens after all the stamens have withered, so that all possibility of self-fertilisation is excluded.

My own observations, made upon plants flowering in my room, differ from Sprengel's in several points. In all the flowers which I examined, the stamens rose up not in pairs but singly, and each was joined by its successor a short time before it withered and fell back; so that when two were erect at the same time, one of them was at the close the other at the commencement of its period. After all the stamens have bent back the stigma ripens, but before it withers the stamens rise up again; and if, through lack of insect-visitors, they still retain a stock of pollen, they shed some of it upon the stigma. So Treviranus' assertion that the approach of the stamens to the stigma takes place for the purpose of self-fertilisation is not quite groundless; but such self-fertilisation takes place only when the flowering time is passing away without insect-visits having taken place.

The whole arrangement of the flower greatly resembles that of *Parnassia*. In both we have fully exposed honey and successive development of the stamens and then of the stigma; in both the conveyance of pollen is insured by the centre of the flower, where an insect is most likely to alight, being occupied successively by a pollen-covered anther and a mature stigma; both are visited by many Diptera and Hymenoptera. But while the white flowers of *Parnassia* are visited by beetles, the yellowish flowers of *Ruta* are altogether avoided by them.

Visitors: A. Diptera—(a) *Stratiomyidæ*: (1) *Sargus cuprarius*, L.; (b) *Syrphidæ*: (2) *Syrphus ribesii*, L., ab.; (3) *S. nitidicollis*, Mgn.; (4) *Melithreptus pictus*, Mgn.; (5) *Ascia podagrica*, F.; (6) *Eristalis sepulcralis*, L.; (7) *Helophilus florens*, L.; (8) *Syritta pipiens*, L., very ab.,—all mainly sucking, but sometimes also eating pollen; similarly (c) *Muscidæ*: (9) *Lucilia silvarum*, Mgn.; (10) *L. cornicina*, F.; (11) *Sarcophaga carnaria*, L.; (12) *S. hæmarrhoa*, Mgn.; (13) *S. albiceps*, Mgn.; (14) *Calliphora erythrocephala*, Mgn.; (15) *Pollenia rudis*, Mgn.; (16) *Sepsis*; (17) *Anthomyia radicum*, L., very ab.; (18) *A. obelisca*, Mgn.; (19) *A. pratensis*, Mgn., (the last three species were determined for me by Herr Winnertz). B. Hymenoptera—(a) *Evaniadæ*: (20) *Fœnus affectator*, F.; (21) *F. jaculator*, F.; (b) *Ichneumonidæ*: (22) various species; (c) *Chrysidæ*: (23) *Chrysis ignita*, L.; (d) *Sphigidæ*: (24) *Crabro elongatulus*, v. d. L. ♀; (25) *Oxybelus bellus*, Dlb.; (26) *Trypoxylon figulus*, L.; (27) *Rhopalum clavipes*, L.; (28) *Agenia punctum*, F. ♂; (29) *Tiphia minuta*, v. d. L. ♂; (e) *Vespidæ*: (30) *Odynerus*

parietum, L. ♀; (*f*) *Apidae*: (31) *Halictus sexnotatus*, K. ♀; (32) *Prosopis sinuata*, Schenk, ♀, freq.; (33) *Apis mellifica*, L. ♀,—all the Hymenoptera only sucking. See also No. 590, II.

*Dictamnus*, L., is visited by humble-bees, whose ventral surfaces come in contact with the reproductive organs of the flower. In the first stage the style lies hidden among the stamens, in the second it is bent outwards with its mature stigma (178, 360, p. 658).

*Correa*, Sm., is proterandrous, according to Delpino (178, p. 170).

#### ORD. CELASTRINEÆ.

85. *EUONYMUS EUROPEA*, L.—The honey is secreted by a fleshy disc surrounding the style, and lies in so thin a layer that it can only be attractive to short-lipped insects. The dull yellow colour of the flowers moreover excludes those insects which are enticed only by bright colours. Like other flowers of the same colour, these are visited only by Diptera and Hymenoptera, and especially by the former; the flies run irregularly over the flowers, attacking the honey-covered surface, now here now there, with their outspread 'end-flaps' (*labellæ*), and in consequence touching anthers and stigmas now with one part of their bodies, now with another. In such circumstances the flowers could only attain regular cross-fertilisation by separation of the sexual organs, either in time or space. Both separations have in fact taken place, and self-fertilisation, which had become unnecessary owing to the abundant insect-visits, has finally become impossible.

The four anthers stand at a distance from the stigma upon stiff filaments, and dehisce directly outwards, while the stigma is still immature and its lobes remain tightly closed. These only separate several days later, and again close up after fertilisation. Thus self-fertilisation cannot take place without the aid of insects; and with their aid only if the earlier days of flowering have passed by without the flower being visited (cf. Delpino, 177).

*E. europæa* is polygamous according to Darwin (167).

Visitors: A. Diptera—(*a*) *Syrphidæ*: (1) *Eristalis tenax*, L.; (2) *Helophilus florens*, L.; (3) *Syrphus ribesii*, L.; (4) *Syritta pipiens*, L.; (5) *Xanthogramma citrofasciata*, Deg. all sucking; (*b*) *Muscidæ*: (6) *Musca domestica*, L.; (7) *Calliphora vomitoria*, L.; (8) *Sarcophaga carnaria*, L., very ab.; (9) *Scatophaga stercoraria*, L.; (10) *Lucilia cornicina*, F.; (*c*) *Bibionidæ*: (11)

*Bibio hortulanus*, L., all sucking; (12) numerous small midges. B. Hymenoptera—*Formicidae*: (13) *Formica* sp. Spiders weave their webs about these flowers to catch the numerous flies. I saw a species of *Vespa* alight and capture a *Sarcophaga carnaria*.

#### ORD. RHAMNEÆ.

*Paliurus aculeatus*, Lam., is distinctly proterandrous, according to Delpino. The stamens are at first erect or inclined slightly inwards, but bend backwards when the stigmas develop. The fertilisers are probably flies of moderate or large size (177).

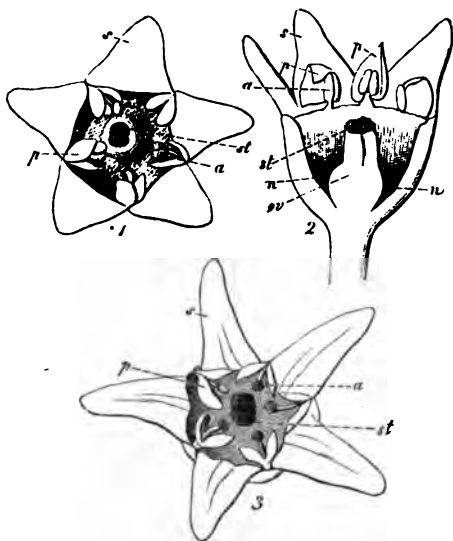


FIG. 50.—*Rhamnus Frangula*, L.

- 1.—Young flower, from above.
  - 2.—Ditto, after removal of the anterior half of the calyx
  - 3.—Older flower, from above.
- s, sepal; p, petal; a, anther; st, stigma; ov, ovary; n, nectary.

86. *RHAMNUS FRANGULA*, L.—The receptacle forms a hemispherical, fleshy disc, which secretes and contains the honey. It is produced at its margin into five triangular white calycine lobes, which are directed obliquely outwards in the flowering period. Between these sepaline lobes, there occur on the margin of the receptacle five small white bi-lobed petals; close below them, and half surrounded by them are five stamens, which are inclined inwards, and dehiscce introrsely.

From the base of the flower rises the ovary ; whose short style is terminated by a bi-lobed stigma below the level of the stamens. When the anthers dehisce, the stigmatic lobes are still small, and probably incapable of fertilisation, but when the stamens wither, they are four times as large as at the commencement of flowering (Fig. 50). The flowers are thus proterandrous. An insect sucking the honey must touch the stamens with one side of its head or proboscis, and the stigma with the other; in this case self-fertilisation cannot occur, though the stigma and anthers ripen at the same time, but cross-fertilisation proceeds regularly. Pollen-collecting insects and sometimes even those sucking honey, if they thrust their heads several times into the same flower, effect self-fertilisation as well as cross-fertilisation.

The honey on account of its open situation is accessible to very various insects, but the flowers are so inconspicuous that they are very little visited. Self-fertilisation can take place if needed, as the stamens on withering may shed their pollen on the now mature stigmas.

Visitors : A. Hymenoptera—(a) *Apidae* : (1) *Apis mellifica*, L. ♀, s. and c.p. ; (2) *Bombus agrorum*, F. ♀ ♀, s. ; (3) *Macropis labiata*, Pz. ♂, s. ; (b) *Vespidae* : (4) *Vespa silvestris*, Scop. ab, s. ; (5) *Eumenes pomiformis*, L., s. B. Diptera—(6) *Culex pipiens*, L. ♂, s.

*Rhamnus lanceolatus*, Pursh., is dimorphic, according to Darwin, but it is not heterostyled in the strict sense (Darwin, 167).

*Rhamnus pumilus*, L.—The size of the flower and the number of its parts is reduced in this species, but the plant is visited by numerous insects. The flower is generally tetramerous, and the petals exhibit all stages of abortion to complete disappearance (609).

*Rhamnus catharticus*, L., is diœcious, with two sub-forms of each sex (167).

#### ORD. SAPINDACEÆ.

*Serjania cuspidata*, St. Hil.—The flower resembles the labiate type, and, like *Paullinia*, L., and *Cardiospermum*, L., is proterandrous.

Many species of *Acer*, according to Delpino, are proterandrous and are fertilised by flies (178, 360).

87. *ÆSCULUS HIPPOCASTANUM*, L.—The arrangement of the flower was thoroughly described by Sprengel. My own notes and

drawings of the horse-chestnut flower, made before I became acquainted with Sprengel's work, differ in one point from his account, and agree with that of Hildebrand. While Sprengel declares that in the younger flowers insect-visitors come in contact only with the stamens because the style is as yet low down, I found just the opposite condition, as the annexed figures show. Although I neglected to compare microscopically stigmas of younger and older flowers, I can hardly doubt that Hildebrand is right in stating the hermaphrodite flowers of the horse-chestnut to be proterogynous. According to Dr. Ogle (632), there occur usually in the lower part of each inflorescence flowers whose anthers fall off without dehiscing although their loculi are full of pollen, and which thus play the part of purely female flowers.

The chief fertilisers are humble-bees; therefore the dimensions of the flower are just such as to suit these insects. The style



FIG. 51.—*Esculus Hippocastanum*.

- 1.—Section of male flower.
  - 2.—Hermaphrodite flower in first (female) stage, seen obliquely from the front.
  - 3.—Section of ditto, in second (male) stage.
- a, anther; n, nectary; ov, ovary; ov' rudimentary ovary; s, sepal; p, petal.

and stamens protrude so far from the flower (in a curve concave superiorly), that a bee on alighting just touches stigma or anthers with the hinder part of his body. The legs fit into the interspaces between the petals, so that the insect finds itself at once in the most convenient position for sucking, and immediately thrusts its proboscis in the direction *n* (1, 3, Fig. 51) into the honey-holding base of the flower. Such a position also permits the insect to fly away very readily, and thus the whole time occupied is reduced to a minimum: alighting, thrusting in the proboscis, and flying away again is the work of a few seconds.

Other bees, whose dimensions do not correspond so well to those of the flowers, have to spend more time over the operation. The humble-bee is also favourably placed for carrying off pollen on the tarsal brushes of the middle and hindlegs. The quick

action of the insects is of as much importance to the plant as to themselves: for the quicker they work, the more young hermaphrodite flowers get fertilised in the same time, with pollen from male flowers or older hermaphrodite flowers; and this in changeable weather is an important consideration.

I have only seen the following humble-bees visiting the horse-chestnut:—(1) *Bombus terrestris*, L.; (2) *B. lapidarius*, L., both species s. and c.p., though I have heard bees humming all day long about the trees in flower in a neighbouring garden. My notes for visitors to this plant refer only to a single afternoon (May 14, 1867). The other visitors noticed were:—(3) *Apis mellifica*, L. ♀, s. and c.p., very ab.; (4) *Eucera longicornis*, L. ♂, s.; (5) *Osmia rufa*, L. ♂, s.; (6) *Haliectus rubicundus*, Christ., ♀, c.p.; (7) *Andrena* sp.

In *Æsculus Pavia* (*rubicunda*), D.C., according to Hildebrand, all the hermaphrodite flowers are proterogynous, as in *Æsculus Hippocastanum*; but the first flowers of each inflorescence are male only, to supply pollen for the opening proterogynous flowers (351).

#### ORD. ANACARDIACEÆ.



FIG. 52.—*Rhus Cotinus*, L.

1.—Male flower.

2.—Hermaphrodite ditto.

3.—Female ditto.

n, nectary.

88. *RHUS COTINUS*, L. (the Wig-tree).—*Rhus Cotinus* shows all possible transitional stages between staminate, hermaphrodite, and pistillate flowers: the first of these are largest, most expanded, and most conspicuous; the last are least so. Hence most insect-visitors come to these flowers in the most advantageous order. (Cf. *Ribes alpinum*, *Salix*, *Bryonia*, *Asparagus*.)

In both staminate and pistillate flowers of *R. Cotinus* traces of the aborted organs remain visible.

The flowers secrete abundant honey on the orange-red fleshy disc surrounding the ovaries, and display it conspicuously. They are visited by numerous insects, chiefly forms with short proboscides. Cross-fertilisation is usually effected even in the

hermaphrodite flowers owing to the wide separation of the stamens and pistil. Like all other flowers of a dull yellow colour they are almost completely avoided by Coleoptera.

Visitors : A. Diptera—(a) *Syrphidæ* : (1) *Helophilus florens*, L., very ab. ; (2) *H. pendulus*, L. ; (3) *Syritta pipiens*, L., very ab., all three s. and f.p. ; (b) *Muscidæ* : (4) *Calliphora erythrocephala*, Mgn. ; (5) *Sarcophaga carnaria*, L. ; (6) *Lucilia cornicina*, F., s., also several undetermined flies and gnats. B. Coleoptera—*Dermestidæ* : (7) *Anthrenus pimpinellæ*, F., licking honey. C. Hymenoptera—(a) *Tenthredinidæ* : (8) *Tenthredo marginella*, Kl. ; (b) *Sphégidæ* : (9) *Oxybelus uniglumis*, L. ; (10) *Gorytes campestris*, L. ; (c) *Vespidæ* : (11) *Eumenes pomiformis*, Spin. ; (12) *Odynerus sinuatus*, F. ; (13) *O. spinipes*, H. Sch. (*quinquefasciatus*, F.), the last six all licking honey ; (d) *Apidæ* : (14) *Andrena albicans*, K. ♀, c.p. ; (15) *Halictus sexstrigatus*, Schenck, ♀ ; (16) *H. sexnotatus*, K. ♀ ; (17) *Apis mellifica*, L. ♂, the last three sucking honey.

89. *RHUS TYPHINA*, L.—I have had little opportunity of watching the flowers of this plant at the proper season. They are very conspicuous, and secrete abundant and easily accessible honey, and the possibility of self-fertilisation is excluded by diœcism. I have as yet only observed the following visitors :—

A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♂, very ab., s. ; (2) *Prosopis communis*, Nyl. ♀ ♂, s. B. Neuroptera—(4) *Panorpa communis*, L. licking honey.

According to Delpino, many species of *Rhus* are proterandrous and fertilised by flies (177).

#### ORD. CORIARIEÆ.

*Coriaria myrtifolia*, L., is markedly proterandrous, according to Hildebrand, and the first flowers are male only (356).

#### ORD. LEGUMINOSÆ.

##### Tribe *Loteæ*.

90. *LOTUS CORNICULATUS*, L.—The structure of the flower of *Lotus corniculatus* is described briefly by Delpino (172, p. 25). He gives it as an example of a papilionaceous flower furnished with a piston-apparatus, and he subsequently compared it fully with *Coronilla Emerus* (178, pp. 39-44). I have devoted especial attention to the fertilisation of these plants, and I shall discuss their structure fully.

The anthers dehisce in the bud, whilst both carina and alæ are still covered by the vexillum, and before any of the petals have nearly attained their full size. At an earlier period the five outer stamens, which alternate with the petals, and the five inner stamens are unequally developed, so that the anthers form two whorls, one behind the other round the style; but when they are ready to dehisce all ten stamens are of equal length, and their



FIG. 53.—*Lotus corniculatus*, L.

- 1.—Front view of flower.
- 2.—Oblique view.
- 3.—Side view, after removal of the vexillum.
- 4.—Flower, seen from above, after removal of the vexillum.
- 5.—Side view, after removal of the alæ, more magnified.
- 6.—From the right side, after careful removal of the right half of the carina.
- 7.—Flower viewed from above, after removal of the vexillum and alæ.
- 8.—The essential organs inclosed in the front half of the carina, as shown in 6, more magnified.
- 9.—Side view of the essential organs from a bud, immediately after the pollen has been shed.
- 10.—A comparison of 8 and 9 shows how much longer and thicker the outer stamens become during the interval between the shedding of the pollen and the opening of the flower.
- 11.—The same organs seen from above, to show how the outer, terminally-thickened stamens spring apart when freed from the pressure of the carina.
- 11.—The nine synadelphous stamens of a fully developed flower spread out.  
*a*, entrances to the honey; *b*, the upward curvature of the free stamens; *c*, the carinal depressions, into which fit the two depressions of the alæ (*c'*); *d*, the five inner stamens, which remain short; *e*, the five outer, which grow long and club-shaped; *f*, stigma; *e-g*, apex of carina, full of pollen; *g*, orifice through which the pollen is expelled.

anthers reach to the base of the conical apex of the carina. The ends of the filaments are still very much alike, but the five outer

show a slight, club-shaped thickening, which afterwards becomes much more apparent; the five inner, including the superior solitary stamen, remain unthickened throughout. The anthers, while yet fully twice as broad as the ends of the filaments, dehisce in the base of the cone, completely filling it with pollen, and when they have discharged their contents they shrivel up to a fourth of their former size. All the petals now grow to their full size, and the five outer stamens elongate and the ends of their filaments thicken, so that, in spite of the continual growth of the carina, they still reach to the hollow cone formed by its apex, and completely fill its lower and wider portion notwithstanding that the five inner stamens have remained behind. When the flower has reached maturity, the essential organs occupy the relative positions shown in 8, Fig. 53. The five inner stamens (*d*) are useless after shedding their pollen, and, far outstripped in development by the other organs, they lie shrivelled up in the lower and wider part of the carina. The five outer (*e*), which have still an important part to play, have continued to grow, and lie with their thickened ends tightly closing in the base of the hollow cone now filled with pollen. Somewhat below the apex of the carina lies the stigma (*f*), and at the apex (near *g*) is a narrow opening; the entire space between the thickened filaments and the orifice is filled with compressed pollen, and thus the piston-mechanism is complete. On the application of a slight downward pressure to the carina, the thickened filaments are forced further into the apical cone of the carina, and squeeze a certain amount of pollen through the orifice in a narrow ribbon. When the pressure ceases, the thickened filaments, thus squeezed together, tend to spring apart, and so raise up the apical cone and restore the whole carina to its former position; the elasticity of the carina itself assists in this action. If the carina be drawn or pressed still further down, the end of the style protrudes, covered with pollen, from the orifice. When the pressure ceases it returns again into the carina; but the edges of the orifice, which readily yield to a pressure from within and allow the stigma and pollen to pass out without hindrance, spring together and scrape off almost the whole of the pollen from the stigma as it returns within the carina.

As soon as the piston-mechanism has become so far complete, the vexillum rises up perpendicularly so as to direct its broad, dark yellow surface straight to the front, and both the alæ arch their surfaces into two hemispheres inclosing the carina, so as to strike the eye equally well from before, from behind, or from either side.

The fleshy thickened base of the coalesced stamens secretes honey on the inner surface, which lies surrounding the base of the ovary and is only to be reached through two small openings on either side of the base of the superior stamen, and the flower is now ready to receive insect-visitors (1, 2, Fig. 53). It only remains to explain how the downward pressure of the carina is effected. This important service is rendered by the *alæ*. They form a platform for the insects, and are so combined with the carina that it is bent downwards along with them. Each *ala* has at the base of its limb a deep depression (3, *c'*), which fits into a corresponding hollow on the upper surface of the base of the carina (5, *c*), and close behind this spot the upper edges of the *alæ* cohere together. If a bee comes, and, whilst clasping the *alæ* with its mid and hindlegs, thrusts its head and forelegs under the vexillum to insert its proboscis into either of the honey-passages, the *alæ* and with them the carina bend downwards, and a quantity of pollen oozes through the tip of the carina and becomes attached to the hairy ventral surface of the bee. If the bee forces its way further into the flower and thus presses the *alæ* and carina down still more, the stigma protrudes from the apex of the carina and rubs against the ventral surface of the insect.

The insect's belly is covered with innumerable pollen-grains from the same and from previously visited flowers, and cross-fertilisation takes place without fail. And it is scarcely possible to doubt, though it is hard to prove by direct observation, that the pollen brought from other flowers is prepotent in its action.

Delpino considers that the stigma does not become capable of fertilisation until its papillæ have been slightly rubbed, by which the stigmatic surface is made sticky. If this view is correct, cross-fertilisation must take place regularly, in the course of repeated visits, since the stigma must be cleared of its own pollen before its papillæ become exposed to friction. In either case it is very much to be desired for the sake of a clear understanding of the mechanism of this flower, that experiments should be instituted to show whether *Lotus* does or does not produce seed when protected from insects.

The process of squeezing out a little ribbon of pollen by depressing the carina may be repeated eight to twelve times, if the carina is pressed down only a little way each time. But bees when collecting pollen press the *alæ* and carina down as far as possible to get all the pollen that they can, so that the supply is exhausted

after a very few visits. Bees, and especially those with abdominal collecting-brushes, are the chief fertilisers of the plant.

Visitors: A. Hymenoptera—(a) *Apidae*: Bees with abdominal collecting-brushes: (1) *Osmia interrupta*, Schenck, ♀ (L. Sld. Thur.); (2) *O. aurulenta*, Pz. ♀ (Sld., Thur.), very freq.; (3) *O. ænea*, L. ♀ ♂, (L.), freq.; (4) *Diphysis serratulæ*, Pz. ♀ ♂ (L. Sld.), freq.; (5) *Megachile Willughbiella*, K. ♀ (L. Sld.); (6) *M. pyrina*, Lep. ♀ ♂, freq.; (7) *M. circumcincta*, K. ♀ ♂ (L. Sld.), ab.; (8) *Anthidium manicatum*, L. ♀ (L.); (9) *A. punctatum*, Latr. ♀ ♂ (Thur), ab.; (10) *A. strigatum*, Latr. ♀ ♂ (Thur.), freq. The females of all these species collect pollen and suck honey at the same time; (b) Bees with femoral and tibial collecting-baskets; (11) *Bombus agrorum*, F. ♀ ♀, s., more rarely c.p.; (12) *B. terrestris*, L. ♀ do.; (13) *Apis mellifica*, L. ♀, very ab., do.; (14) *Eucera longicornis*, L. ♀ ♂, very ab., only s.; (15) *Rhopites canus*, Eversm. ♀ ♂ (Thur.), s.; (16) *Andrena labialis*, K. ♀, s.; (17) *A. xanthura*, K. ♀, c.p.; (18) *A. convexiuscula*, K. ♀, s. and c.p.; (19) *Halictus rubicundus*, Chr. ♀, s. and c.p.; (20) *H. flavipes*, K. ♀, s.; (c) Cuckoo-bees: (21) *Nomada ruficornis*, L. ♀, s.; (22) *Cœlioxys*, sp. ♂, s. B. Diptera—(a) *Conopidae*: (23) *Conops flavipes*, L. (4—5), s. only observed once,—thrusting its tongue beneath the vexillum; (b) *Syrphidae*: (24) *Melanostoma mellina*, L., b.p. C. Lepidoptera—(a) *Rhopalocera*: (25) *Lycæna Icarus*, Rott., s.; (26) *Hesperia tages*, L. s.; (27) *H. alveolus*, H. s.; (b) *Sphinges*: (28) *Sesia empiformis*, E. (Thur.), s.; (29) *Zygæna loniceræ*, Esp. (Thur.), s.; (c) *Bombyces*: (30) *Porthesia auriflua*, S. V. (sucking vainly for honey); (d) *Noctua*: (31) *Euclidia glyphica*, L., s. Lepidoptera and Conops thrust their tongues beneath the vexillum without perceptibly depressing the carina; they were therefore quite useless for fertilisation.

Twenty-seven additional visitors (19 *Apidae*, 5 *Lepidoptera* 3 *Diptera*) are recorded in my *Weitere Beobachtungen*, II. p. 246.

Altogether, I have observed upon Lotus:—

	<i>Apidae</i> .	<i>Lepidoptera</i> .	<i>Diptera</i> .	Total.
In Low Germany... ..	17	25	1	43
On the Alps ... ..	41	12	3	56

That is to say, in each hundred species of visitors there are:—

	<i>Apidae</i> .	<i>Lepidoptera</i> .	<i>Diptera</i> .	Total.
In Low Germany... ..	39·5	58·1	2·3	99·9
On the Alps ... ..	73·2	21·4	5·2	99·9

91. ANTHYLLIS VULNERARIA, L.—*Anthyllis vulneraria* belongs to the group of papilionaceous flowers with piston-mechanism, but it differs so strikingly from *Lotus* in many points that it deserves a special description.

The very long claws of the petals are surrounded by a calyx, 9 to 10 mm. long, somewhat swollen in the middle and covered with soft hairs (1 *a*, Fig. 54). From this the vexillum projects to a distance of 6 to 7 mm., inclined obliquely upwards; a groove on the lower part of its blade (7 *b'*) receives the alæ, and two rounded lobes at its base (7 *d*, *d*) clasp round them inferiorly, so that the alæ are completely embraced by the vexillum.



FIG. 54.—*Anthyllis vulneraria*, L.

- 1.—Flower from below.
  - 2.—Ditto, from the side, after removal of the calyx.
  - 3.—Ditto, from above: the vexillum also has been removed.
  - 4.—Anterior half of the carina seen obliquely from the left side and above.
  - 5.—Anterior half of carina and the right ala.
  - 6.—Lower side of left ala: the claw is cut short.
  - 7.—Vexillum from below (1—7  $\times 3\frac{1}{2}$ ).
  - 8.—Apex of carina, after removal of its left half ( $\times 7$ ).
- a*, calyx; *b*, under side of vexillum; *b'*, its groove; *c*, upper (outer) surface of vexillum; *d*, lobes of vexillum which grasp the alæ and carina; *e*, inner, *f*, outer, sides of ala; *g*, deep narrow groove on the outside of the vexillum, visible inside as a sharp ridge; *h*; *t*, hollow in the upper surface of the carina (*h*), into which the ridge *h* fits; *t*, sharp process or tooth of the carina, which fits into a hollow *h'*, behind the ridge *h*; *m*, carinal orifice, at which the pollen emerges; *m'*, anterior infolding of the upper border of the ala; *n*, column; *o*, entrance to the honey; *p*, thickened ends of the filaments; *q*, empty withered anthers; *r*, pollen; *s*, stigma; *t*, claws of the alæ.

An insect which tries to reach the honey at the base of the flower must grasp the sides of the alæ and thrust its proboscis (at least 9 to 10 mm. long) under the vexillum.

The alæ surround the carina, and are so connected with it that when the alæ are depressed the carina is forced down with them. This connection is formed in three ways: (1), a deep narrow groove (3, *g*) exists at the base of each ala, appearing on the inner side as

a sharp ridge (5, 6, *h*) which fits into a groove on the carina (4, 5, *i*); (2), a sharp triangular tooth (4, 5, *l*) is borne by the carina behind this groove, and catches in the space (5, 6, *h'*) behind the ridge on the inner surface of the ala; and (3), the upper borders of the alæ are folded inwards for a short space (3, 5, 6, *m'*), and at this fold they cohere together above the carina. Close in front of the spot where the upper borders of the alæ are thus firmly applied to each other, the apex of the carina emerges when the alæ are pressed down. The upper margins of the carina are coherent except at the apex, where they leave a longitudinal slit, and when the carina (along with the alæ) is depressed, there emerges from this slit a ribbon-shaped mass of pollen, pressed forwards by the thickened ends of the ten stamens (8, *p*).

When the pressure is removed the alæ and carina return to their former position; when they are again pressed down another portion of pollen is pressed out. After the greater part of the pollen has been squeezed out in this way, the stigma (8 *s*) emerges at the same slit; it has lain imbedded in pollen in the carina but emerges free from it, for its papillæ are not yet adhesive and the pollen-grains are scraped off by the edges of the slit.

If the stigma is rubbed with slight pressure over a glass plate a line of moisture marks its course; if it be now brought in contact with pollen, the pollen adheres to it so firmly that it is not easily removed. Doubtless the same effect is produced by insect-visits; the flower gives up pollen to the ventral hairs of its first visitors; and after its pollen is spent, the superficial cells of the stigma coming in contact with the insect get ruptured and exude their fluid contents; pollen from other flowers, with which the insect is already dusted, now adheres to the stigma and the act of cross-fertilisation is complete. Whether in absence of insects the flower is fertilised by its own pollen has still to be decided by a simple experiment. I observed the following bees fertilising this plant near Mühlberg in Thuringia, July 11th to 14th, 1868:—

(1) *Bombus silvarum*, L. ♀ (10<sup>1</sup>), s.; (2) *B. hortorum*, L. ♀ (21), s.; (3) *B. muscorum*, F. ♀ (13—14), s.; (4) *Osmia aurulenta*, Pz. ♀ (8—9), c.p., (all very frequent). I also saw *Lycæna alsus*, W. V. ♀, and a *Capsus* vainly attempting to suck the honey. I have seen it visited on the Alps by 12 species of bees, and 10 of Lepidoptera (609).

*Dorycnium (Bonjeania) hirsutum*, Ser.—According to Delpino, the flower has a piston-action, and the ends of the filaments are thickened (179, p. 45).

<sup>1</sup> These numbers in brackets indicate the length of the insect's proboscis.

Tribe *Trifoliæ*.

92. *ONONIS SPINOSA*, L.—This plant also has flowers with a piston-mechanism, which however differ materially both from *Lotus* and *Anthyllis*. They are devoid of honey, and, like almost all the honeyless *Papilionaceæ*, monadelphous, for the separation of the superior stamen in other forms is only useful in giving access to the honey. The alæ, which serve as in most other *Papilionaceæ* for bees to alight on, and as levers to depress the carina, embrace the upper part of the carina (3, Fig. 55) and are united to it by two projections directed downwards and forwards (5 *d*), which fit into deep grooves in the two halves of the carina. Two lobes at the base of the upper borders of the alæ (3, 6, *e*) directed backwards, but not pouched, lie over the staminal column without touching it,

FIG. 55.—*Ononis spinosa*, L.

- 1.—Essential organs from a bud.
  - 2.—Ditto, from a flower ( $\times 7$ ).
  - 3.—Flower, from the side, after removal of calyx and vexillum.
  - 4.—Some stamens, more magnified, to show the difference between the outer and inner filaments.
  - 5.—Left ala, from the inside.
  - 6.—Ditto, from the outside.
- a*, outer, *b*, inner stamen; *c*, pollen, seen through the carina; *d*, alar processes pointing downwards and forwards; *e*, lobe of the upper border of the ala, pointing backwards.

and can give little help in keeping the parts in their proper places. The two alæ never cohere with one another.

The upper borders of the carina cohere at first, leaving a small opening at the tip, and the pollen is squeezed out as in *Lotus*. But sooner or later after repeated depressions this suture ruptures, and now if the carina be depressed the anthers themselves emerge. If the carina was not thrust down too far they return within the carina when the pressure is relieved; but if the carina was pressed violently down, as it frequently is by bees, the anthers remain along with the stigma partly or wholly exposed.

We must, therefore, take young flowers, to see the squeezing out of the pollen. Thus the flowers of *Ononis* afford a stage intermediate between *Lotus* with its piston-mechanism, and *Melilotus* in which the reproductive organs simply emerge from the carina.

In regard to the formation of the "piston," *Ononis* stands between *Lotus* and *Anthyllis*. In *Lotus* the five outer filaments, which alternate with the petals, are thickened at their ends to express the pollen; in *Anthyllis* the ends of the filaments are all thickened alike; in *Ononis* they are all thickened, but the outer whorl much more so than the inner. While the outer stamens thus perform the function of a piston to a greater extent than the inner, the inner (1 *b*) produce pollen in much larger amount than the outer (1 *a*). This is an interesting step towards separation of the two whorls of stamens for two distinct purposes.

Though the flowers of *Ononis* possess no honey they are visited by numerous bees, but in the number of their visitors they are far behind *Lotus*, which has abundant honey. It is curious that not only female bees but males also often visit several flowers in succession and perform all the actions of sucking. They have obviously no outward token of the lack of honey, but must discover it by experience. The females, after making sure that there is no honey, take to collecting pollen; the males, on the other hand, abandon the flowers after a few vain attempts, though they may remain some time about the plant in pursuit of the female. The visitors are exclusively bees, and mainly forms with abdominal collecting-brushes.

A. Bees with abdominal collecting-brushes: (1) *Osmia aurulenta*, Pz. ♀ (Thur.), ab.; (2) *O. aenea* L. ♀, freq.; (3) *Megachile versicolor*, Sm. ♀ (Haar); (4) *M. pyrina*, Lep. ♀ ♂, freq.; (5) *M. circumcincta*, K. ♀, ab.; (6) *M. maritima*, K. ♀; (7) *Anthidium manicatum*, L. ♀ ♂, ab.; (8) *A. punctatum*, Latr. ♀ ♂; (b) Bees with tibial pollen-baskets: (9) *Apis mellifica*, L. ♀; (10) *Cilissa leporina*, Pz. ♀; (11) *Anthophora quadrimaculata*, Pz. ♀ ♂, ab. (Thur.); (12) *Bombus lapidarius*, L. ♀; (13) *B. terrestris*, L. ♀.

*Ononis repens*, L., is also visited exclusively by bees (590, II. p. 254).

According to Bentham, most species of *Ononis* in southern Europe are liable to abortion of the corolla in spring, and cleistogamic self-fertilisation then takes place (399, p. 67; 531, p. 312).

*Parochætus*, Ham., has cleistogamic flowers, according to Kuhn.

93. *MEDICAGO SATIVA*, L.—Although the mechanism of this flower has been several times the subject of careful study, it is by

no means fully explained yet. I hope at least to advance our knowledge of the means by which the elastic tension of the parts is produced and controlled. *Medicago sativa* has, like *Sarothamnus scoparius* and *Genista tinctoria*, explosive flowers. As in these latter, the staminal column before explosion is inclosed within the carina, whose upper edges cohere together; and when an insect presses down the carina the column not only emerges but springs violently up and is unable to return to its former place. As in *G. tinctoria*, the reproductive organs after explosion are pressed against the vexillum and are not affected by further insect visits. But *Medicago sativa* differs from these two plants by having both the elastic tension and the force which restrains it localised in different parts of the flower.



FIG. 56.—*Medicago sativa*, L.

- 1.—Young (virgin) flower from below.
  - 2.—Ditto, from above, after removal of the vexillum and the upper half of the calyx.
  - 3.—Inner view of right ala.
  - 4.—Carina seen obliquely from above.
  - 5.—Exploded flower seen obliquely from above; the vexillum and upper half of the calyx have been removed ( $\times 84$ ).
- a, calyx; b, vexillum; c, ala; d, its claw; e, invaginated process of ala, directed inwards and forwards; f, its external opening; g, digitate process or lobe of ala, directed inwards and backwards; h, carina; i, invaginated pouches in the carina, which receive the alar processes, (e); k, the coherent filaments; l, the upper free stamen; m, entrances to the honey; n, anthers; o, stigma.

While in *Sarothamnus* it is the style only which acts as a spring, in *Genista tinctoria* the column tends to spring upwards, and the alæ and carina together tend to spring downwards. In *Medicago sativa* the elastic tension resides almost exclusively in the upper stamens. This can be shown clearly by dividing the upper from the lower stamens, whereupon the upper part of the bundle curves still more strongly upwards, and the lower part sinks down till it stands almost horizontal.

In *Medicago sativa* it is not the coherent upper margins of the

carina, as in *Sarothamnus* and *Genista*, which prevent the column from springing up in the young flower, though these margins are coherent here also, but we may separate them completely from one another without explosion taking place. The structures which prevent it are two pairs of projections developed on the petals of the carina and alæ, which lie upon the column.

Two are directed forwards, and consist of deep pouches in the superior basal angles of the carina (*i*, 4, 5) which meet in the middle line above the column. Into these fit still deeper pouched processes of the alæ (*e*, 2, 5), which both connect the alæ firmly with the carina, and also help to strengthen the hold upon the column. These anterior pouches of the alæ (*e*, 2, 5) are only a further development of those shallow depressions by means of which the alæ are united to the carina in *Trifolium* and *Melilotus*.

Besides this anterior pouch, each ala possesses at the base of its upper border a long finger-shaped process, which is directed backwards, and is a further development of that which we shall see appearing in *Melilotus*. The two processes (*g*, 2, Fig. 56) curve upwards and inwards so that their ends almost meet in the middle line above the staminal column.

If in a young flower we cut through the claw of the carina, the column springs upwards to some extent, carrying with it the carina and alæ. If in another unexploded flower we carefully cut through one of the digitiform processes of the alæ, the parts remain motionless; but on cutting the process of the other side explosion at once follows. The pouched processes of the carina (*i*) are thus not sufficient to hold the column down without the aid of the processes (*g*) of the alæ, nor are the latter sufficient after section of the carina. Explosion can therefore be effected equally well by separating the anterior pouches (*e*, 2), by separating the digitiform processes (*g*, 2), or, finally, by depressing the alæ and carina. If an insect inserts its proboscis in the middle line between the anterior pouches and the digitiform processes, or if it stands upon the alæ and thrusts its head in the middle line under the vexillum, in either case explosion follows. The stigma (*o*, 5) projects beyond the anthers, and, therefore, is the first to strike the under surface of the bee's body or proboscis; an instant later the anthers come in contact with an area close around the spot that the stigma touched, dusting it with fresh pollen. The first flower that the insect visits is, of course, not cross-fertilised, but as the bee withdraws from the flower self-fertilisation inevitably occurs. Self-fertilisation is undoubtedly efficient, for Hildebrand has shown that

flowers which wither unexploded when insects are excluded produce seed by self-fertilisation.

In spite of their very accurate mechanism, I have observed by watching insect-visitors that the flowers have two imperfections. In the first place they continue to secrete honey after explosion, and in the second, the young unexploded flowers very frequently permit insects to obtain the honey without performing any service in return.

It is plain that the continued secretion of honey after explosion is detrimental to the plant; for it leads the insects to visit exploded flowers instead of restricting their visits to flowers that require their aid. I have seen hundreds of hive-bees sucking honey on exploded flowers, thrusting the proboscis laterally over one of the alæ, and not coming in contact at all with the stigma or anthers, which were pressed close up against the vexillum.

The other imperfection is also taken advantage of by the hive-bee, as Henslow has remarked. The bee probably finds it unpleasant to have its proboscis struck by the exploding column at each visit; for it prefers, even in the case of young flowers, to insert its proboscis laterally close to one of the alæ, so that no explosion results. Although hive-bees are by far the most numerous visitors of this flower, I have never seen them effect explosion; but I have often observed them from a short distance acting in the manner just described. Though I have frequently watched this plant, I have never succeeded in seeing explosion actually performed, though the number of exploded flowers that we meet with shows that it must take place very frequently. Butterflies visit the flowers in great numbers, and it is doubtless by them that explosion and cross-fertilisation are effected; but they are generally too wild to permit close observation of their movements. Once I had a good view of *Hesperia thauwas*, Hufn., sucking a young unexploded flower, but like the bees it inserted its proboscis from the side and did not cause explosion. A fine needle inserted in the middle line of the flower causes explosion, and the thin proboscis of a butterfly is undoubtedly sufficient to do the same.

A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s., very freq.; (2) *Megachile pyrina*, Lep., s. B. *Lepidoptera*—(a) *Rhopalocera*: (3) *Pieris brassicæ*, L.; (4) *P. rapæ*, L.; (5) *P. napi*, L., all three ab.; (6) *Vanessa urticæ*, L.; (7) *Colias hyalæ*, L.; (8) *Satyrus hyperanthus*, L.; (9) *Lycæna argiolus*, L.; (10) *Hesperia thauwas*, Hufn.; (b) *Noctuæ*: (11) *Plusia gamma*, L. Fifteen additional visitors (eleven *Apidae*, three *Lepidoptera*, and *Bembex rostratus*) are recorded in No. 590, II.

94. *MEDICAGO FALCATA*, L.—Though on the whole the flower of this species resembles that of *M. sativa*, it possesses certain peculiarities which facilitate explosion, and make it more difficult for bees to obtain the honey without releasing the column. For the pouches directed forwards and the processes directed backwards on the alæ grasp the column less firmly, as may be seen in 2, Fig. 57, so that a less pressure is followed by explosion; but on the other hand a thin proboscis can pass more easily to the base of the flower without bringing about explosion. The alæ leave less room for a proboscis to enter, as they are shorter and broader and rest on the



FIG. 57.—*Medicago falcata*, L.

- 1.—Flower, viewed obliquely from above.
  - 2.—Ditto, after removal of calyx and vexillum, from above.
  - 3.—Left ala.
  - 4.—Carina.
  - 5.—Exploded flower, after removal of vexillum, seen obliquely from the right and above; the column appears considerably foreshortened.
- a, calyx; b, vexillum; c, pathfinder; d, claw of ala; e, lamina of ala; f, invaginated process of ala, directed forwards; g, lobe of ala directed backwards; h, coherent claws of carina; i, coherent laminae of ditto; k, carinal pouches, which receive the processes f; l, column; m, superior free stamen; n, entrances to the honey; o, stigma. ( $\times 7$ .)

carina for a shorter space in their basal half. Accordingly, of the very many bees which I observed on flowers of *M. falcata*, I did not see one sucking or collecting pollen on unexploded flowers without releasing the column, but I saw many Lepidoptera sucking without causing explosion. The flowers of *M. sativa* seem fitted rather for fertilisation by Lepidoptera, and those of *M. falcata* rather for fertilisation by bees. And my lists may lead us to conclude that the flowers of *M. sativa* offer special attractions for Lepidoptera, and

those of *M. falcata*, on the other hand, for bees; yet I am not able to account for this difference in attractiveness.

Visitors, at Rehmsberg, Thuringia, July, 1868:—

A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s., freq.; (2) *Bombus muscorum*, F. ♀, s.; (3) *Rhophites canus*, Ev. ♀ ♂, s.; (4) *Cilissa leporina*, Pz. ♀ ♂, s. and c.p.; (5) *Andrena denticulata*, K. ♀, s.; (6) *A. fulvicrus*, K. ♀, s.; (7) *Halictus quadricinctus*, F. ♀, c.p.; (8) *Nomada Solidaginis*, Pz. ♀, s.; (9) *N. varia*, Pz. ♀, s.; (10) *N. ferruginata*, K. ♀, s.; (11) *Osmia aurulenta*, Pz. ♀, s. and c.p., ab. B. Diptera—(a) *Bombyliidae*: (12) *Systæchus sulfureus*, Mik., s.; (b) *Syrphidae*: (13) *Helophilus trivittatus*, F. C. Lepidoptera—(a) *Rhopalocera*: (14) *Hesperia*, s.; (15) *Lycæna*, s.; (b) *Sphinges*: (16) *Sesia asiliformis*, Rott., s.; (17) *Zygæna carniolica*, Esp., ab.; (c) *Noctuæ*: (18) *Euclidia glyphica*, L., s. Four additional visitors (*Lepidoptera*) are recorded in No. 590, II.

95. *MEDICAGO LUPULINA*, L.—The flowers of this species, whose upper stamens seem to possess very little elasticity, are exceedingly minute but yet attract many diligent visitors.

A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s., very freq. (It is characteristic of the honey-bee that it does not disdain even this flower's tiny store of honey. The whole inflorescence is pulled down by the weight of the bee, which then sucks the flowers head downwards. It sucks a few flowers, at most four, on one inflorescence, and then flies away to another plant of the same species); (2) *Andrena convexiuscula*, K. ♀, s.; (3) *A. xanthura*, K. ♀, c.p.; (4) *Halictus flavipes*, K. ♀, c.p.; (5) *Bombus agrorum*, F. ♀ ♀, s. B. Diptera—*Conopidae*: (6) *Myopa buccata*, L., s.; (7) *M. testacea*, L., s. C. Lepidoptera—*Rhopalocera*: (8) *Thecla rubi*, L. ♀, s.

Darwin also saw *M. lupulina* visited abundantly by bees. He found the plants very much less fertile when protected from insects by a net.

96. *MELILOTUS OFFICINALIS*, Willd.—The mechanism of the flower resembles that of *Trifolium repens*, with certain slight variations.

The calyx is much shorter (only 2 mm. long) and at the same time wider, thus admitting insects with shorter tongues to the honey, and also giving greater range of movement to the petals. The alæ and carina can rotate much farther downwards, since their claws are not adherent to the staminal column as in *T. repens*. Their return to their former place when relieved from pressure is insured by two finger-like processes (*f*) which replace the pouches of *T. repens* at the superior basal angle of the alæ; they grasp the staminal column superiorly, and, when the carinæ are drawn down, they separate slightly but still remain closely applied to the

staminal column ready to spring back and grasp it as firmly as before. The stigma projects further beyond the anthers

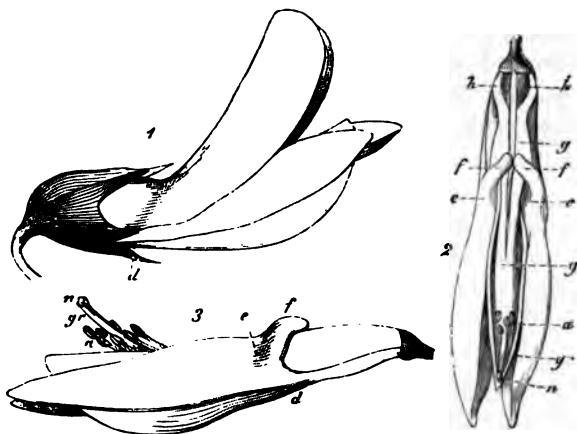


FIG. 58.—*Melilotus officinalis*, Willd.

- 1.—Flower, from the side.  
 2.—Ditto, from above, after removal of calyx and vexillum.  
 3.—Ditto, from the side, after depression of the ala and carina.  
 a, anthers; d, point of flexure of carina; e, depressions in the ala, whose inner surfaces are connected with the outer surfaces of the carinal petals by interdigitation of their cells; f, digitate processes of the superior basal angles of the ala; g, column; h, entrances to the honey; gr, style; s, stigma.

than in *T. repens*, so that self-fertilisation is rendered even more unlikely.

Visitors: Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀ very freq., s. and c.p.; (2) *Andrena dorsata*, K. ♀, s. and c.p.; (3) *Heriades truncorum*, L. ♀, c.p.; (4) *Coelioxys quadridentata*, L. ♂, s.; (5) *Osmia* sp.; (b) *Sphegidae*: (6) *Ammophila sabulosa*, L. ♂, s.; (c) *Tenthredinidae*: (7) *Tenthredo* sp., vainly seeking honey.

97. *MELILOTUS VULGARIS*, Willd (*M. alba*, Thouill.).—This species is visited by the honey-bee, which I have found in hundreds busy sucking honey and collecting pollen on the plant: also by *Macropis labiata*, Pz., and by *Empis livida*, L.

98. *TRIFOLIUM REPENS*, L.—The floral mechanism is here simpler than in *Lotus*, and is one of the simplest to be found among *Papilionaceæ*. Stamens and pistil are inclosed in the carina; when the latter is pressed down they protrude, but they return within it when the pressure is removed, and the pollen is thus protected from the weather and from robbery. As in all other *Papilionaceous* flowers which contain honey, the honey is secreted

by the bases of the cohering stamens, it surrounds the base of the ovary, and can only be reached through two apertures, one on either side of the base of the superior free stamen. An insect, to reach the honey, must thrust its head in beneath the vexillum, and must stand in doing this upon the two alæ. In climbing on to the alæ and thrusting its head below the vexillum, it forces up the latter and presses the alæ and carina down; and the reproductive organs, protruding from the carina, are forced up against the ventral surface of the insect. The organs all return to their

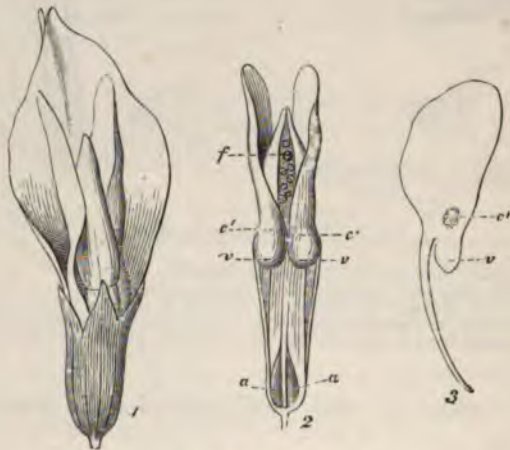


FIG. 59.—*Trifolium repens*, L.

- 1.—Flower, from below.
- 2.—Ditto, from above, after removal of calyx and vexillum.
- 3.—Inner view of right ala.  
c', pouched swelling.

former place when the insect leaves the flower; and cross-fertilisation takes place regularly, since the stigma projects slightly beyond the anthers and therefore comes first in contact with the ventral surface of the insect.

In addition to these characters, which *Trifolium repens* possesses in common with many other Papilionaceous flowers, the following are peculiar to itself: (1) the arrangements for excluding certain short-lipped insects; (2) the conditions of rotation of the alæ and carina; (3) the provisions for bringing back the parts of the flower to their former place when pressure is removed.

(1) The calyx-tube, which surrounds the claws of the petals and limits the movements of the vexillum and alæ, is only 3 mm.

long; so that the less specialised bees, such as *Andrena* and *Halictus*, are not shut out from the honey.

(2) The alæ cohere with the carina at one point on each side (c', 2, 3, Fig. 59), so that both rotate upwards and downwards together; this rotation is facilitated by the very thin and weak claws of the alæ and carina, which adhere for the greater part of their length to the staminal tube, but are free anteriorly. Since the alæ project considerably beyond the carina, they play the part of a long lever-arm in this action. The long anterior end of the vexillum has a similar action.

(3) The return of the parts to their original position is brought about chiefly by the vexillum and the alæ, in addition to the part played by the calyx-tube. The strong, broad claw of the vexillum overlaps the other petals and the reproductive organs, being closely applied to them above and at the sides; by its elasticity it returns forcibly to its own place after it has been moved, and forces the organs within into their place also; the anterior part of the staminal column is also kept in check by the alæ, whose superior basal lobes are modified into two vesicles (v) which lie close together upon the upper part of the column.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, very ab., s. and c.p.; (2) *B. pratorum*, L. ♀, s.; (3) *Megachile Willughbiella*, K. ♂; (4) *Halictus tarsatus*, Schenck, ♀, s.; (5) *H. maculatus*, Sm. ♀, c.p.; (6) *Andrena fulvicrus*, K. ♀, s. B. Diptera—(a) *Syrphidæ*: (7) *Volucella bombylans*, L., s.; (b) *Conopidæ*: (8) *Myopa buccata*, L., s.; (9) *M. testacea*, L., s. C. Lepidoptera—*Rhopalocera*: (10) *Pieris brassicæ*, L., s. Of these visitors it is only the bees that act in the manner described and effect cross-fertilisation regularly; the other visitors only do so occasionally. See also No. 590, II., and No. 609.

The Dutch Clover was one of the first Papilionaceous flowers in which the necessity of insect-visits for full productiveness was demonstrated. Darwin found that when insects were excluded by means of a fine net the plant was only one-tenth as productive as when insects were freely admitted (152).

99. *TRIFOLIUM FRAGIFERUM*, L.—This species agrees generally in the characters of its flower with *T. repens*; but the flowers are much smaller, the calyx-tube is only 2 mm. long, and the alæ are bent outwards. I have seen the hive-bee visiting its flowers abundantly. Though the hive-bee as a rule keeps very strictly to one species of flower for a time, yet, where *T. fragiferum* and *T. repens* grow together, it visits the flowers of both indiscriminately.

100. *TRIFOLIUM PRATENSE*, L.—The honey lies at the base of a tube, 9 to 10 mm. long, formed by cohesion of the nine inferior stamens with each other and with the claws of the petals; it is secreted by the bases of the stamens, and accumulates in the tube around the base of the ovary. But while in *Trifolium repens*, as in *Lotus* and most other *Papilionaceæ*, only two small openings, one on either side of the base of the superior stamen, give access to the honey, and compel the bee to thrust its proboscis down to them outside the staminal tube, in *T. pratense* the bee's proboscis, after being thrust under the vexillum, passes at once into the staminal



FIG. 60.—*Trifolium pratense*, L.

- 1.—Flower, from below.
  - 2.—Ditto, from above, after removal of the vexillum.
  - 3.—Anterior part of flower, twice as much magnified; the edges of the carina have been forced apart.
  - 4.—Right ala, from within.
  - 5.—Right half of the carina, from without. (The claws of 4 and 5 have been broken short off.)
  - 6.—The essential organs emerging from the depressed carina.
- a, calyx; b, tube formed by coalescence of the nine filaments with the claws of the vexillum, ala, and carina; c, vexillum; d, concave part of the inner side of the ala; e, lower border of ala, bent outwards; f, outward surface of ala; g, pouched swelling on the base of the ala; h, carina; i, style; k, superior free stamen; l, stigma; m, anthers; n, point of union between ala and carina; o, point of flexure of the carina; p, part of the upper border of the ala, bent outwards; q, downward extension of vexillum.

tube, to which in this case the claws of the petals are adherent. The insect's proboscis, passing down the tube in the middle line superiorly, would be impeded by the superior stamen which is inclosed in the tube if this retained its normal position; but its two ends only are situated in the middle line, and the rest of the stamen lies wholly to one side.

From the anterior end of the common tube come off the

various organs as follows: (1) The broad base of the vexillum, which is continuous with the superior and lateral portions of the tube, and even with part of its inferior aspect by means of an expansion (*q*) just at the base of the free limb. (2) The base of the carina, which is attached to the inferior part of the edge of the tube in the interval left by the vexillum: though not half so broad as the base of the vexillum, it is broad and strong enough to return quickly to its place after being bent downwards. (3) The two alæ, whose flexible claws spring from the common tube; the lamina of each bulges out at its base (*g*), more distinctly than in *T. repens*, to cover over the top of the staminal column and help to keep it and the petals in their proper relative positions. (4) The staminal tube, which is split superiorly to admit the free tenth stamen, and which divides in the hollow of the carina into stiff filaments which curve upwards and are slightly thickened at their ends.

In the midst of the stamens lies the style curving upwards till its stigma slightly overtops the anthers.

If now a bee inserts its proboscis beneath the vexillum, while it clings with its forelegs on to the alæ (which are coherent with the carina) resting its middle and hind legs on a lower part of the inflorescence, the carina and alæ are drawn downwards, and the stigmas and anthers are thrust up against the under side of the bee's head; the stigma, standing highest, receives the pollen brought by the bee, and instantly afterwards the anthers dust the bee with fresh pollen. Cross-fertilisation is thus insured; self-fertilisation may take place as the bee draws back its head, but is probably neutralised and superseded by the immediately preceding cross-fertilisation.

In order to reach the honey in this way, an insect must possess a proboscis at least 9 to 10 mm. long. The pollen is accessible to all insects which can press down the carina, and it is clear that bees when collecting pollen on the flower perform cross-fertilisation as well as when sucking honey. The red clover, like most flowers whose honey lies more than 7 to 9 mm. deep, is liable to the attacks of *Bombus terrestris* and other insects which use the holes that *B. terrestris* has made. The small flowers of clover become conspicuous by aggregation into heads, and contain very abundant honey.

- A. Hymenoptera—*Apidae*: 1 *Bombus agrorum* L. ♀ proboscis 14 mm. 2 (2) *B. lapidarius* L. ♂ ♀ 10–14 " 3 *B. ruderarius* L. ♂ ♀ 10–13 " 4 *B. agrorum* F. ♂ ♀ 10–15 " 5 *B. lucorum* L. ♂ ♀ 14–15 " 6 *B.*

confusus, Schenck, ♀ ♀ (12—14) ! (7) *B. muscorum*, F. ♀ (13—14) ! (8) *B. fragrans*, K. ♀ (15) ! (9) *B. (Apathus) rupestris*, F. ♀ (14) ! (10) *B. vestalis*, Fourc. ♀ (12) ! (11) *B. campestris*, Pz. ♀ (10—12) ! (12) *B. Barbutellus*, K. ♀ (12) ! all s., some also c.p. ; (13) (*Bombus terrestris*, L. [7—9]), bites through the tube and so reaches the honey with some delay,—it has, however, the advantage of obtaining honey even from unexpanded flowers ; (14) (*B. pratorum*, L. ♀ [8]), behaves in the same way) ; (15) *Apis mellifica*, L. ♀ (6), usually visits the red clover only for its honey, which its proboscis is not able to reach in the legitimate manner,—yet I have now and then seen hundreds of honey-bees on a patch of red clover, all busy collecting pollen ; (16) *Anthophora pilipes*, F. ♀ (19—20), s. ! (17) *Eucera longicornis*, L. ♀ ♂ (10), s. ! (18) *Cilissa leporina*, Pz. ♀ (3½), c.p. ! (19) *Andrena xanthura*, K. ♀ (3), c.p. ! (20) *A. Schrankella*, Nyl. ♀ (4) ; (21) *A. fulvicrus*, K. ♀ (3½) ; (22) *A. fasciata*, Wesm. ♀ ♂ (3—4),—all three sought in vain for honey, their collecting-hairs remained free from pollen ; (23) *Colletes fodiens*, K. ♀ (2½), c.p. ! (24) *Halictus flavipes*, K. ♀ (2½), c.p. ! (25) *Anthidium manicatum*, L. ♀ ♂ (9—10), s. ! (26) *Megachile circumcincta*, L. ♀ (11), s. and c.p. ! (27) *Osmia ænea*, L. ♀ (9—10), s. and c.p. ! (28) *Diphysis serratulæ*, Pz. ♀ (7—8) c.p. ! *B. Diptera*—(*a*) *Bombyliidæ* : (29) (*Systæchus sulfureus*, Mikan [6—7]) ; (*b*) *Syrphidæ* : (30) (*Volucella bombylans*, L. [7—8]) ; (*c*) *Conopidæ* : (31) (*Sicus ferrugineus*, L. [6—7]),—I have seen all these three flies thrusting their tongues beneath the vexillum, though their tongues are too short to reach the honey in the legitimate way). *C. Lepidoptera*—(*a*) *Rhopalocera* : (32) *Pieris brassicæ*, L. (15) ; (33) *P. rapæ*, L. ; (34) *Vanessa urticæ*, L. (12) ; (35) *Satyrus Megæra*, L. ; (36) *S. Janira*, L. ; (37) *Hesperia sylvanus*, Esp. ; (38) *H. thaumas*, Hfn. ; (*b*) *Noctuæ* : (39) *Plusia gamma*, L., all s.

*Trifolium badium*, Schreb.—The flower is in like manner adapted for Lepidoptera. On the Alps I found it visited by four Apidæ and eleven Lepidoptera (609).

*Trifolium alpestre*, L.—The flower is similarly arranged, and was seen to be visited by two species of Apidæ and nine Lepidoptera (*Weit. Beob.* II.).

Kuhn describes cleistogamic flowers in *Trifolium* (399), and *T. polymorphum* is cleistogamic according to Darwin (*Forms of Flowers*, 2nd ed.).

*Trifolium alpinum*, L., *T. pallescens*, Schreb., and *T. nivale*, Sieb. (*T. pratense*, L., var. *nivale*), are described in my *Alpenblumen* (No. 609).

101. *TRIFOLIUM ARVENSE*, L.—The tube is hardly 2 mm. long.

Visitors : *A. Hymenoptera*—(*a*) *Apidæ* : (1) *Apis mellifica*, L. ♀ ; (2) *Bombus Rajellus*, Ill. ♀ ♀, very freq. ; (3) *B. lapidarius*, L. ♀ ; (4) *Cilissa leporina*, Pz. ♀ ; (5) *Andrena xanthura*, K. ♀ ; (6) *Halictus zonulus*, Sm. ♀ ; (7) *H. quadricinctus*, F. ♀ ; (8) *Colletes marginata*, Sm. ♂ ; (9) *Diphysis serratulæ*, Pz. ♂ ; (10) *Osmia cæmentaria*, Gerst. ♂ (Thur.) ; (11) *Megachile maritima*, K. ♂, all sucking only ; (*b*) *Sphegidæ* : (12) *Psammophila affinis*, ♀, s. *B. Lepidoptera*—(13) *Hesperia thaumas*, Hfn., s.

102. *TRIFOLIUM RUBENS*, L. (Thuringia, Rehmburg near Muhlberg).—This species shows certain adaptations for Lepidoptera as well as for bees; I have found it visited by six species of *Bombus* and *Anthophora*, and by seven species of *Lepidoptera*.

103. *TRIFOLIUM FILIFORME*, L. :—

Visitors :—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. ; (2) *Halictus albipes*, F. ♂, s. ; (3) *H. cylindricus*, F. ♀, c.p. *Lepidoptera* : (4) *Lycæna ægon*, s.v.s.

104. *TRIFOLIUM MEDIUM*, L. :—

Visitors : *Apidæ* : (1) *Andrena dorsata*, K. ♀, c.p. ; (2) *Bombus agrorum*, F. ♀, sucking normally. Eleven additional visitors are recorded in No. 590, II.

105. *TRIFOLIUM PROCUMBENS*, L. :—

Visitors : *Apidæ* : (1) *Apis mellifica*, L. ♀, s. ; (2) *Halictus flavipes*, K. ♀, s. Five additional visitors are recorded in No. 590, II.

106. *TRIFOLIUM MONTANUM*, L.—I have found this species visited in Low Germany by four *Apidæ*, one *Sphægidæ*, and four *Lepidoptera* (590, II.) ; on the Alps by eight *Apidæ* and eight *Lepidoptera* (609). Besides the adaptations to bees usual in *Papilionaceæ*, it shows an adaptation to cross-fertilisation by *Lepidoptera*, the closely folded vexillum bringing the insect's proboscis in contact with the stigma and anthers.

*Genistææ.*

107. *LUPINUS LUTEUS*, L.—The flowers of *Lupinus luteus*, like those of *Ononis spinosa*, are devoid of honey and are provided with a piston apparatus; they present the following peculiarities :—The alæ are coherent with one another at the anterior border, and each possesses a lateral fold near its base, fitting into a depression in the carina. They surround the carina as in *Lotus*, but are flat instead of being strongly convex, and since the sides of the vexillum are bent backwards the flower is more conspicuous from the side than from the front. The division of labour which began to be marked in *Ononis* between the two whorls of stamens, one whorl producing the pollen, the other pressing it forwards, is much more complete in *Lupinus* (1, 2, Fig. 61). The anthers of the five outer stamens are much larger than those of the inner; they dehisce within the bud, while the others are much shorter and very far from maturity (1, Fig. 61); and then after placing their pollen in the apex of the carina, they wither

completely, and remain in the wide lower part of the carina (2, Fig. 61). The five inner anthers now begin to grow rapidly, and squeeze the pollen in the point of the carina more by means of their anthers, which remain spherical, than by the thickened ends of their filaments; they thus do the work of a piston, except the superior stamen (1), which remains inferior to the others in length and thickness.



FIG. 61.—*Lupinus luteus*, L.

1.—Essential organs, from a bud; the outer anthers are dehiscing.

2.—Ditto, from a flower.

2, 4, 6, 8, 10, the five outer; 1, 3, 5, 7, 9, the five inner stamens; x, stigma.

The spherical stigma is surrounded at its base, like that of the Laburnum, by a ring of stiff erect hairs which prevent or limit the application of its own pollen.

I have noticed only the following visitors:—

Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♂, ab., c.p.; (2) *Bombus lapidarius*, L. ♂, scarce, c.p.; (3) *Megachile circumcincta*, K. ♀, c.p.

The flower of *Lupinus albus* differs in certain points from the preceding species (cf. Delp. 178, pp. 46, 47).

*Lupinus*, sp.—Mr. Swale observed that in New Zealand cultivated varieties of *Lupinus* were unfertile unless he released the stamens with a pin. In England, according to Darwin, the Lupines are fertilised by humble-bees, not by hive-bees (152).

108. *GENISTA TINCTORIA*, L.—In the young bud the ten stamens are distinctly seen to form two whorls (1, Fig. 62). The five anthers of the outer whorl (2, 4, 6, 8, 10 in 1, Fig. 62), overtop those of the inner, and the four superior ones are the first to

ripen. In the bud, they are already on the point of dehiscing, while those of the inner whorl have attained scarcely a quarter of their full size. The ten stamens, and the style, which projects far beyond them, are all inclosed by the carina, whose two petals cohere along both their upper and lower margins. As the four superior anthers of the outer whorl dehiscence introrsely and then wither, their pollen remains lying above the style, which courses along the lower edge of

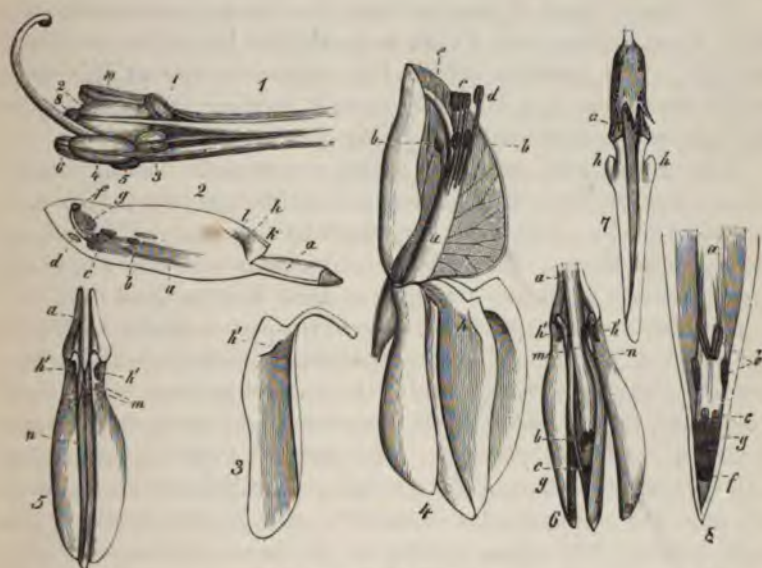


FIG. 62.—*Genista tinctoria*, L.

- 1.—Essential organs from a young bud.
  - 2.—Position of the parts inclosed in the carina of a young (virgin) flower.
  - 3.—Inner view of right ala.
  - 4.—Exploded flower.
  - 5.—Young (virgin) flower, from above, after removal of calyx and vexillum.
  - 6.—Ditto, after the carina has been cleft to near its apex by pressure, from above.
  - 7.—Young flower, from above, after removal of vexillum and ala.
  - 8.—Anterior half of a young flower, cleft so far that explosion must result; from above, twice as much magnified.
- a, column; b, the four outer stamens, which remain short (2, 4, 8, 10, in Fig. 1); c, the five inner stamens (1, 3, 5, 7, 9); d, the stamen of the outer whorl which remains below the style; e, tip of style; f, stigma; g, pollen; h, lateral fold of carina into which a fold (h') of the corresponding ala fits; h', non-coherent part of the upper borders of the carinal petals; m, ala; n, carina, ends of filaments; q, empty, shrivelled anthers; r, pollen; s, stigma; tt, claws of ala.

the carina, and it gets pushed forward into the apex of the still elongating carina by the inner stamens which quickly extend beyond the now empty outer stamens. The inferior stamen of the outer whorl (6 in 1, Fig. 62), which lies immediately below the style, remains closed when the other four dehiscence, and it grows to the same length as the five inner stamens and dehiscence with them.

If it dehisced along with the other four stamens of its own whorl and then withered, its pollen would lie useless in the lower part of the carina, a little in front of its middle point, and would never be pressed forward; but since it grows to the same length as the inner stamens and dehisces simultaneously with them, its pollen unites in great part with that of the two neighbouring stamens (5 and 7 in 1, Fig. 62), and is heaped with it above the style.

The inner whorl of stamens and the inferior stamens of the outer whorl dehisce and wither a short time before the vexillum expands. The position which the organs occupy at this time within the carina may be easily seen by holding the carina up to the light, and is represented in 2, Fig. 62.

The carina still forms a much compressed sheath, closely surrounding the style and the pollen of all the ten stamens which is heaped above it. It is kept horizontal by the action of two equal and opposite forces. The column of stamens with the contained style possesses a tension upwards, so that if it be freed from the surrounding petals it springs up close to the perpendicular vexillum. The claws of the alæ and of the two petals which form the carina possess a downward tension, and if the upward pressure of the style is removed, they suddenly bend downwards and place the alæ and carina in a vertical position. The alæ are kept in connection with the carina by means of a bulging protuberance at the base and near the upper border of each (*h'*, 3, 5, 6), which lies in the angle between the upper border of the carina and another protuberance directed outwards and upwards from each half of the carina near its base (*h*, 7).

The opposite tensions balance one another so long as the upper borders of the carina cohere together (*n*, 5) and the pouched lobes of the alæ (*m*, 5) meet one another above the staminal column.

As soon, however, as an insect places its feet upon the alæ and thrusts its head beneath the vexillum, the pouched lobes of the alæ slip down below the staminal column (*m*, 6); at the same time the union between the upper borders of the carina is ruptured from behind forwards by the pressure of the essential organs in its posterior part, and as soon as the splitting reaches the tip of the style the two opposite forces are set free, and the staminal column springs upwards while the alæ and carina spring downwards. If we hold the flower in one hand, and press down the tip of the carina with a needle or a pencil-point, we see clearly the split spreading forwards, and the pouched lobes of the alæ separating, so that the

flower passes from the young, closed state (Fig. 62, 5) to the half-opened state (Fig. 62, 6); if we press a little harder, the split passes forward beyond the tip of the style (Fig. 62, 8), and in the same instant the column flies upwards to the vexillum, scattering a cloud of pollen, and the alæ and carina spring down into the vertical position.

If an insect performs the above operation while standing on the alæ and thrusting its head beneath the vexillum, the column is prevented from springing up to its full height; it cannot scatter a cloud of pollen into the air, but the ascending style forces its stigma and instantly afterwards the mass of pollen against the under side of the insect. If the insect has been dusted with pollen in a previously visited flower, cross-fertilisation is thus effected; if not, the stigma is dusted with its own pollen as the insect creeps backwards out of the flower. Whether self-fertilisation occurs in absence of insects is a point that has still to be settled by experiment. Specimens with young virgin flowers which I left standing in water for over fourteen days withered without either exploding or producing seed.

Since the flowers contain no honey, and expend all their pollen in a single explosion, after which the staminal column and style are concealed by the vexillum which closes over them as in the bud, they can only offer attractions for pollen-collecting insects, viz.: female bees busy with the care of their young; and even these are only permitted a single visit. The flowers, however, are visited by very various insects, which fly away after a vain attempt to obtain pollen or honey. I observed the following visitors in sunny weather in July, 1869, on a stretch of land covered with *G. tinctoria* near Brilon and Warstein:—

A. Hymenoptera—(a) *Apidæ*: (1) *Megachile circumcincta*, K. ♀, very ab., c.p.; (2) *M. centuncularis*, L. ♀, very ab., c.p.,—the males occasionally seek in vain for honey; (3) *M. villosa*, Schenck, ♀, one specimen, c.p.; (4) *M. versicolor*, Sm. ♀, freq.; (5) *M. Willughbiella*, K. ♂; (6) *Diphysis serratulæ*, Pz. ♂; (7) *Anthidium punctatum*, Latr. ♂,—the last three come in vain search for honey; (8) *Apis mellifica*, L. ♀, ab., c.p.; (9) *Bombus terrestris*, L. ♀, scarce, c.p.; (10) *Colletes Daviesiana*, K. ♀, c.p.; (11) *Andrena albicans*, K. ♂; (12) *A. fulvescens*, Sm. ♂,—both vainly seeking honey; (13) *A. xanthura*, K. ♀; (14) *A. fulvicrus*, K. ♀; (15) *Halictus rubicundus*, Chr. ♀; (16) *H. albipes*, F. ♀; the last four scarce, c.p. (all, including the honey-seeking males, caused the flowers to explode, and effected cross-fertilisation). (b) *Vespidæ*: (17) *Odynerus trifasciatus*, F. ♀. B. Diptera—(a) *Conopidæ*: (18) *Sicus ferrugineus*, L.; (19) *Myopa testacea*, L.; (b) *Syrphidæ*: (20) *Chrysotoxum bicinctum*, L. C. Lepidoptera—*Rhopalocera*: (21) *Satyrus Megæra*,

L.—the last five obtained neither honey nor pollen, and did not cause the flowers to explode. D. Coleoptera—*Chrysomelidæ*: (22) *Cryptocephalus sericeus*, L.; (23) *Cr. vittatus*, F.; (24) *Cr. morsei*, L., feeding on the tissues of the flower. Four additional visitors are recorded in No. 590, II.

This list is of special interest, as it shows that flower-loving insects do not restrict themselves by hereditary instinct to those flowers which are most useful to them, but that they search widely for their food in flowers, and so very often seek in vain.

Of the pollen-collecting bees, those with abdominal collecting-brushes have the easiest work, since the explosion of the flower forces the pollen directly on to the collecting-hairs; they are also the most useful to the plant, as they fly from flower to flower with least loss of time.

109. *GENISTA ANGLICA*, L.—In this species the opposed tensions of the column on the one hand and the alæ and carina on



FIG. 63.—*Genista anglica*, L.

- 1.—Young (virgin) flower, from the side.
- 2.—Ditto, from the front.
- 3.—Inner view of right ala.
- 4.—Exploded flower; the style is less recurved than usual.
- 5.—Exploded flower from the left; a more normal specimen than 4.

the other are much less marked. When the flower explodes, the carina and alæ move only a short way downwards, and the whole column does not bend upwards, but only the style, whose tip curves inwards also. The only visitors that I have noticed are bees with tibial and femoral collecting-baskets. But it would be premature to conclude, even in the case of *G. tinctoria*, that because its flowers are chiefly plundered and fertilised by bees with abdominal brushes, they have been specially adapted only for those bees.

I had a most favourable opportunity of watching the actions of the hive-bee on flowers of *G. anglica* one sunny morning, May 3, 1871. It was the first sunshine after long-continued rain,

and so all the flowers were still unfertilised. The bees flew humming from one flower to another, clung by their legs to the alæ, and thrust their heads with outstretched proboscis beneath the vexillum while the abdomen hung down. While the head and its proboscis were thus placed just as if they were sucking honey from the base of the flower, the midlegs were in active movement, scraping pollen into the baskets on the hindlegs. On May 14, 1871, I again watched the hive-bee at work, when most of the flowers had now exploded. A single bee flew on to ten or twenty plants, whose flowers had all been fertilised, without stopping on any flower. At last it found a young unfertilised flower, on which it eagerly descended. This long search and occasional descent upon young unfertilised flowers was frequently repeated; but sometimes I saw a bee, after seeking in vain for young flowers, settle on an old exploded one, and insert its proboscis as if the flower contained honey. Sometimes also I saw a hive-bee visit a young flower without causing it to explode.

Besides the hive-bee, I have only seen *Andrena fulvicrus*, K. ♀, *A. nigro-aenea*, K. ♀, and *Halictus cylindricus*, F. ♀, collecting pollen on this plant, all very frequently.

110. *GENISTA PILOSA*, L.—The mechanism of this flower is like that of *G. anglica*. It has been thoroughly described by Delpino, who found the plant sterile to its own pollen (178, 360). I have only seen the honey-bee collecting pollen on it.

111. *CYTISUS LABURNUM*, L.—In the flowers of *Cytisus Laburnum*, as in those of *Melilotus* and *Trifolium*, the reproductive organs simply emerge from the carina and return within it. The connection of the alæ with the carina is not a firm one, being formed simply by a shallow bulging depression in each ala (e, l) which fits into a corresponding depression on the side of the carina; yet this is quite sufficient, as a slight pressure suffices to depress the alæ and carina. The elasticity of the carina is small; it is sufficient to bring the carina back to its original place after repeated slight depressions, but not sufficient if the carina be pressed far down. Accordingly, after repeated visits of humble-bees the essential organs protrude freely from the slit.

The flowers are characterised by a peculiar kind of proterandrous dichogamy. Immediately before the bud expands, the stigma lies in the apex of the carina surrounded by transparent, stiff, erect hairs; these overtop the stigma, and in the young flower they

bend over its papillar surface, protecting it from immediate contact with the insect-visitor. Gradually these hairs wither, so that in older flowers the stigmatic papillæ are freely exposed (5, Fig. 64), and at the same time the style bends more and more inwards, so that the stigma protrudes farther and farther from the carina. Cross-fertilisation is thus insured and self-fertilisation prevented in case of insect-visits, while spontaneous self-fertilisation is also prevented in absence of insects.

The most remarkable peculiarity in the flowers of the *Laburnum* is that, like those of *Orchis mascula*, *O. morio*, &c., they only supply nectar inclosed in cellular tissue. The ordinary secretion of honey and the ordinary means of access to the honey



FIG. 64.—*Cytisus Laburnum*, L.

1.—Basal part of an old flower, seen from above, after removal of calyx and vexillum.

2, 3, 4.—Stigmata of younger flowers.

5.—Stigma of an old flower.

*aa*, cut base of calyx; *b*, point of insertion of vexillum; *c*, fleshy eminence, anterior to insertion of vexillum, which is probably probed by insects; *d*, claw of ala; *e*, shallow pouched depression of ala, which fits into a corresponding depression on the upper surface of the carina; *f*, carina; *g*, its cleft.

are here wanting, and the stamens are monadelphous; but in front of the point of attachment of the vexillum is a thick, fleshy swelling, so rich in honey that if a fine glass tube be inserted in it a column of clear fluid ascends the tube. The vexillum is marked with dark lines pointing towards the base of the flower, which can only be interpreted as pathfinders, and an insect's proboscis inserted beneath the vexillum comes without fail to the nectary. I have seen both bees and butterflies inserting their tongues into numerous flowers in succession, spending some time on each; the bees had their pollen-baskets empty, and were therefore not engaged in collecting pollen. It seems therefore impossible to doubt that the swelling at the base of the vexillum is actually pierced by bees and butterflies for the sake of its secretion.

A. Hymenoptera—*Apidae*: (1) *Bombus lapidarius*, L. ♀ ♂, sometimes s., sometimes c.p.; (2) *B. terrestris*, L. ♀, s.; (3) *Andrena atriceps*, K. ♀ ♂, s.; (4) *A. albicans*, K. ♀, c.p.; (5) *A. xanthura*, K. ♀, c.p.; (6) *Apis mellifica*, L. ♀, c.p., very ab. B. Lepidoptera—*Noctua*: (7) *Plusia gamma*, L., s., freq. C. Coleoptera—*Nitidulidae*: (8) *Meligethes*, creeping about within the flowers.

*Cytisus sagittalis*, Koch, is visited by bees only; I have noted eight different species upon its flowers (590, II.).

In *Cytisus canariensis*, L., and *C. albus*, Link., according to Hildebrand, the carina bends down slightly under pressure, and the anthers and style first move slightly downwards with it, and then spring upwards so that the pollen flies out and part of it is applied without fail to the stigma (No. 346). It is, however, hardly conceivable that such an action effected by insects should lead only to self-fertilisation.

112. *CYTISUS (SAROTHAMNUS) SCOPARIUS*, Koch.—The flowers, like those of our species of *Genista*, are explosive and devoid of honey. Darwin noticed that the flowers do not explode spontaneously, and scarcely set a single capsule if protected from insects; but that when an insect visits the flower, first the short stamens explode, dusting it with pollen below, then the longer stamens, dusting it above, and that finally the pollen applied to the under side of the insect by the shorter stamens fertilises those stigmas which are not covered with pollen at the moment of explosion.

I have observed the way in which insects operate on the flower most closely in the case of the hive-bee. The bee, on alighting, grasps the alæ with its mid and hindlegs, thrusting its forelegs and head below the middle of the vexillum. The alæ and with them the carina are thus pressed forcibly down, and the united upper margins of the carina split asunder from behind forwards. [The alæ are connected with the carina by means of a fold (f, 4b) which catches in the angle between the upper edge of the carina and the sharp pouched protuberance at its side (f, 4, 4c, 6)]. As soon as the split has extended midway, the five shorter stamens spring out; they had dehisced in the bud, pressing their pollen against the closed upper edge of the carina (5, Fig. 65), and now they force part of their pollen against the under side of the bee. The shock is not enough to drive the bee away; at most it pauses for a moment, and then resumes work with increased diligence. The split now quickly extends further, and it has scarcely reached the place where the tip of the style lies than a second and much



FIG. 65.—*Sarothamnus scoparius*

- 1.—Young (virgin) flower, from the side.
- 2.—Ditto; the vexillum is rather more erect, and shows the stamens.
- 3.—Ditto, after removal of the vexillum, from above.
- 4.—Ditto, after removal of the alae also.
- 4b.—Left ala, from the inside, showing the concavity *f*, with the carina.
- 4c.—The convex swelling of the carina, viewed from the front.
- 5.—Position of the essential organs in the young flower.
- 6.—Flower after explosion of the short stamens, from the side.
- 7.—Position of the parts after complete explosion.
- 8.—Staminal tube, slit open immediately to the right of the stigma.

against its back, it stays for some seconds motionless as though stunned, and then turns round, freeing itself from the style, and begins to gather pollen upon the anthers with its mouth and legs.

The behaviour of humble-bees is on the whole similar to that of the hive-bee. But while the hive-bee is only strong enough to cause the flower to explode, often causing only the shorter stamens to escape, humble-bees are able easily to force open any flower in which the vexillum has become erect; and they may be seen not unfrequently to break open, though with considerable effort, flowers in which the *alæ* are still inclosed by the vexillum.

Cross-fertilisation is insured, since the stigma is always mature in flowers capable of exploding, and since the bee's back is always touched by the stigma an instant before the fresh pollen is applied to it. And even the flower to which the bee pays its first visit, and whose stigma is not pollinated in the first instance, has a fair chance of being fertilised subsequently, as the style curls round so far as to bring the stigma again uppermost. A second visitor can therefore easily apply pollen to it from the same or from another flower, and the flower is certain to be again visited. I have only occasionally seen hive-bees and humble-bees visit exploded flowers, but the pollen that they leave is gleaned by the smaller bees, flies, and beetles, which are not strong enough to force open the young flowers. I have found females of *Andrena fulvicrus*, K., *Halictus zonulus*, Sm., and *Osmia fusca*, Chr., busily collecting pollen on exploded flowers; *Rhingia rostrata* and the beetles *Meligethes* and *Anthobium* are often to be seen feeding on these remnants of pollen. There is no doubt that many flowers of *Sarothamnus*, which have been exploded by bees not yet dusted with pollen, are fertilised by such supplementary visitors. The shorter stamens which apply their pollen to the under sides of bees or of *Rhingia*, and the position of the stigma after explosion when it also is liable to come in contact with the under surfaces of insects, stand in close relation with this supplementary process of fertilisation.

In the Broom as in Laburnum, the vexillum is marked in its lower part by dark lines coursing towards the base of the flower. If the flower contained honey, these lines could only be explained as pathfinders, but here the flowers have neither any free honey nor a nectariferous swelling such as exists in and round the insertion of the vexillum in Laburnum. In this case the dark lines may either be a useless inheritance from ancestors whose flowers

contained honey, or else they may be of use to the plant by leading bees which visit it for the first time to expect honey and accordingly to perform the actions necessary for exploding the flower. When the explosion occurs, the bee finds its hopes of honey gone, but its labour is repaid by such an abundant store of pollen that it proceeds to visit other flowers merely to collect pollen.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀! very ab.; (2) *Bombus lapidarius*, L. ♀! (3) *B. terrestris*, L. ♀! both ab.; (4) *B. agrorum*, F. ♀! (5) *B. hortorum*, L. ♀! (6) *Andrena fulvicrus*, K. ♀; (7) *Haliectus zonulus*, Sm. ♀; (8) *Osmia fusca*, Christ. ♀, all c.p. (those marked (!) forced the flowers open). B. Diptera—*Syrphidae*: (9) *Rhingia rostrata*, L., f.p., ab. C. Coleoptera—(a) *Staphylinidae*: (10) *Anthobium*, f.p.; (b) *Nitidulidae*: (11) *Meligethes*, f.p.

*Ulex europæus*, L., has explosive flowers, which, according to Dr. Ogle's description, agree essentially with those of *Genista tinctoria* (633).

*Amorpha fruticosa*, L., and *A. canescens*, Nutt.—The carina and alæ are abortive; the stamens and style are exserted. The small flowers, devoid of a platform for insects, are arranged in a spike, on which bees can easily creep from flower to flower. The flowers are proterogynous, with persistent stigmas. They are cross-fertilised, according to Beal, by bees and wasps, which work upwards beginning at the bottom of the spike (41, 178, 590, II.).

*Indigofera*.—According to Hildebrand's figures and description (346), the flowers are so far explosive that the carina and alæ flap downwards, while the reproductive organs remain erect; self-fertilisation takes place as the flower withers. Henslow (323) described the flowers of *I. speciosa* with reference to Hildebrand's description, and maintained justly that their structure was only intelligible on the supposition that it led to cross-fertilisation.

*I. macrostachya*, Vent., was seen by Delpino to be visited by *Bombus italicus* (178).

113. *CORONILLA EMERUS*, L.—Delpino has thoroughly described in the case of this flower the piston-apparatus which we have studied in *Lotus corniculatus*. As visitors he observed *Bombus*, *Anthophora pilipes*, *Eucera longicornis*, and *Xylocopa violacea*.

114. *CORONILLA VARIA*, L., resembles *Lotus corniculatus* in regard to its piston-apparatus, but the flower contains no honey; it is nevertheless diadelphous (178, p. 45). In Thuringia I have seen it visited abundantly by hive-bees.

Mr. T. H. Farrer discovered that honey occurs on the fleshy

outer surface of the calyx. He found that bees obtained this honey in the following manner: they alighted on the flowers in the usual way, and inserted their tongues as usual beneath the vexillum; then, however, the proboscis came through the wide interspace which is left between the unusually narrow claws of the petals, and so reached the outer side of the calyx. The same holds good of *Coronilla montana*, Scop., *C. glauca*, L., and *C. minima*, L. (244).

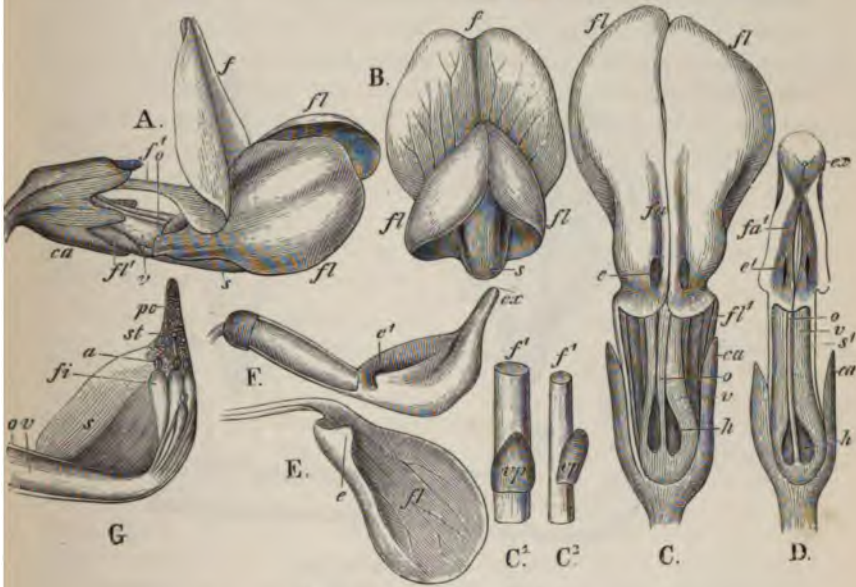


FIG. 66.—*Hippocrepis comosa*, L.

- A.—Flower, from the side ( $\times 4$ ).  
 B.—Ditto, from the front.  
 C.—Ditto, after removal of the vexillum and the upper part of the calyx, from above ( $\times 7$ ).  
 C<sup>1</sup>.—Part of the claw of the vexillum, from below.  
 C<sup>2</sup>.—Ditto, from the side; *vp*, process which closes the entrance to the honey.  
 D.—The same flower (C), after removal of the ala also.  
 E.—Inner view of right ala.  
 F.—Carina, from the side.  
 G.—Ditto, in section, more magnified.  
*a*, anthers; *ca*, calyx; *e*, pouched depression in the ala, fitting into the corresponding depression *e'* in the carina; *ex*, terminal orifice of carina; *f*, vexillum; *f'*, its claw; *fa*, fold of ala which fits into the corresponding fold *fa'* of the carina; *fl*, filament; *fl'*, claw of ala; *o*, superior free stamen; *ov*, ovary; *po*, pollen; *s*, carina; *st*, stigma; *v*, coherent filaments.

115. *HIPPOCREPIS COMOSA*, L.—This flower resembles that of *Lotus* in the way in which the pollen is pumped out (178, 360), but it is characterised by the peculiar way in which the honey is concealed.

The claw of the vexillum is so narrow and so much curved (A) that one can see between it and the stamens. On the under side

of its base it bears a flattened triangular process (*vp.* C<sup>1</sup> C<sup>2</sup>) which fits exactly over the nectaries (*h*) and closes them with considerable firmness. A bee visiting the flower can only obtain the honey by using the vexillum as a long lever to raise up this lid; and to do this it must insert its head beneath the vexillum, and consequently effect cross-fertilisation.

On the Alps I observed various bees cross-fertilising the plant, and also numerous Lepidoptera which visited the flowers but only effected cross-fertilisation occasionally (609).

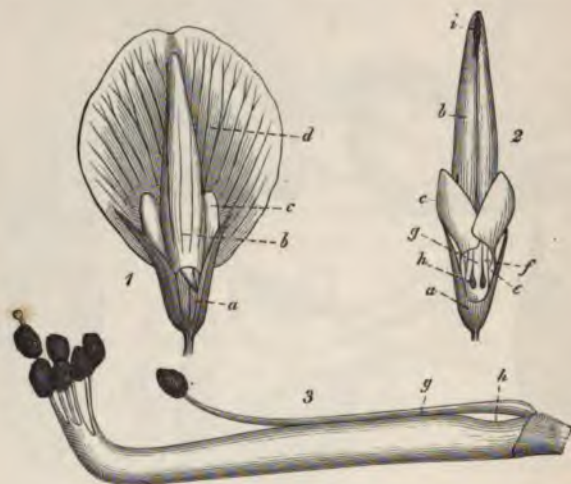


FIG. 67.—*Onobrychis sativa*, Lam.

- 1.—Flower, from below ( $\times 3$ ).
  - 2.—Ditto, after removal of the vexillum and the upper half of the calyx, from above.
  - 3.—Essential organs, from the side ( $\times 7$ ).
- a*, calyx; *b*, carina; *c*, ala; *d*, vexillum, pale red with darker lines (*pathfinders*); *e*, claw of ala; *f*, coherent filaments; *g*, free stamen; *h*, entrance to honey; *i*, cleft of carina, through which the anthers and stigma emerge.

116. *ONOBRYCHIS SATIVA*, Lam.—The flower has the same simple structure as we have studied in the case of *Melilotus* and *Trifolium*: when the carina is depressed, the stigma and the anthers (which dehisced in the bud) emerge, and when the pressure is removed the carina springs up and again incloses these organs. The arrangement in this case is still simpler than in the two above-named genera, since the carina performs by itself the functions which the alæ formerly shared with it; for the alæ are very much reduced, only covering the claw of the carina, and serving to prevent or to render difficult the removal of honey at either

side. The carina alone forms the platform for insects to alight on, and the lever by which its own downward rotation is effected: its own elasticity brings it back to its former position on removal of the pressure.

Cross-fertilisation is insured, in case of insect-visits, by the prominence of the stigma, which must touch the under surface of an alighting insect in advance of the anthers. In absence of insects, self-fertilisation cannot occur, especially as the style continually grows, so that in older flowers it protrudes for a distance of 1 to  $1\frac{1}{2}$  mm. beyond the carina. The brightly coloured flowers, massed in racemes, attract numerous insects. The calyx-tube is only 2 to 3 mm. long; the broad vexillum ascends at a very small angle from the horizontal, and is the better fitted to serve as a fulcrum against which the bee may place its head while thrusting down the carina with its legs. Both honey and pollen are thus rendered accessible to short-lipped bees. In sunny weather the flowers are the resort of so many insects that they can well afford to dispense with the power of self-fertilisation.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀ (6), s. and c.p.; so abundant as to make nine-tenths of all the visitors; (2) *Bombus senilis*, Sm. ♀ (14—15); (3) *B. silvarum*, L. ♀ (12—14); (4) *B. agrorum*, F. ♀ (12—15); (5) *B. confusus*, Schenck, ♀ (12—14); (6) *B. terrestris*, L. ♀ (7—9); (7) *B. muscorum*, F. ♀ ♀ (10—14); (8) *B. pratorum*, L. ♀ ♀ (8— $11\frac{1}{2}$ ); (9) *B. Scrimshirani*, K. ♀:—all sometimes suck honey, sometimes collect pollen; (10) *B. (Apathus) rupestris*, F. ♀ (12—14), s.; (11) *B. campestris*, Pz. ♀ (10—12), s.; (12) *Eucera longicornis*, L. ♂ ♀ (10—12), s. and c.p.; (13) *Andrena labialis*, K. ♀ ♂, s. and c.p.; (14) *A. nigroænea*, K. ♂ (3); (15) *Halictus albipes*, F. ♀ (3), s. and c.p.; (16) *H. flavipes*, F. ♀, s. and c.p.; (17) *H. lugubris*, K. ♀; (18) *Megachile circumcincta*, K. ♀, s. and c.p.; (19) *Osmia aurulenta*, Pz. ♀ (8—9), s. and c.p. (Thur.); (20) *O. spinulosa*, K. ♀ (Thur.); (21) *Chalicodoma muraria*, F. ♀ (10), s. and c.p. (Thur.); (22) *Cœlixys conoidea*, Ill. ♀, s. B. Diptera—*Syrphidae*: (23) *Volucella plumata*, L. (7—8). C. Lepidoptera—(a) *Rhopalocera*: (24) *Pieris napi*, L., s.; (25) *Lycæna* sp.; (b) *Sphinges*: (26) *Zygæna carniolica*, Scop. (Thur.); (c) *Noctuæ*: (27) *Euclidia glyphica*, L.; (28) *Plusia gamma*, L., ab.,—all sucking, but apparently not effecting fertilisation. See also No. 590, II.

*Stylosanthes*, Swartz, *Arachis*, L., *Heterocarpæa*, Phil., *Lespedeza*, Rich., and *Chapmannia*, Torr. and Gr., have cleistogamic flowers according to Kuhn.

*Errum lens*, L., is visited by the honey-bee and by Lepidoptera (590, II.).

*Vicia hirsuta*, Koch, is remarkable for the great simplification of the whole mechanism of the flower, in relation to its great reduction in size (590, II.).

117. *Vicia Cracca*, L.—The Vetches afford an instance of how much caution is needed before drawing conclusions for a whole genus from a single species. Delpino describes a brush of hairs upon the style as a character of the genus *Vicia*, without mentioning what species he observed it in (178); but his description applies only vaguely to *V. sepium*, and not at all to *V. Cracca*. In other peculiarities of structure the Vetches which I have examined show remarkable diversity.

In *V. Cracca* the style is very short (about  $1\frac{1}{2}$  mm. long), and for some distance below the stigma it is covered with long, slanting hairs (5, Fig. 68). Though the hairs are longer and closer on the outer side than on the inner, they form a cylindrical brush rather



FIG. 68.—*Vicia Cracca*, L.

- 1.—Flower, from the side ( $\times 3$ ).
  - 2.—Ditto, after removal of calyx and vexillum, from above, a little more magnified.
  - 3.—Ditto, after removal of the ala also.
  - 4.—Inner view of left ala.
  - 5.—Style, highly magnified.
- a, b*, anterior and posterior infoldings of the superior border of the ala; *a', b'*, corresponding depressions in the carina; *c*, process, a lobe of the superior border of the ala, directed backwards and inwards; *d*, claw of ala; *e*, claw of carina; *f*, swollen point of the carina, containing the pollen; *g*, superior basal lobes of carina; *h*, honey; *p*, brush; *o*, orifice for exit of style; *st*, stigma.

than a basket (*cestella*) as Delpino describes them. The anthers, which lie close round the brush of hairs, dehisce and shed their pollen upon the hairs when the flower has scarcely attained half its full size; and the stigma, which is overtopped all round but especially on the outer side by hairs, is also covered with pollen. The brush of hairs, thus covered above and all round with pollen, lies in a pouch of the flattened tip of the carina (*f*, 2, 3), and emerges when the carina is depressed from the narrow slit at its tip.

As in other Papilionaceæ, the carina is depressed by means of the alæ, which are firmly connected with it and which serve as long levers on which the insect alights.

Each ala is connected at two points with the margin of the

**carina.** In the middle of its upper border, each ala has a small but deep fold (*a*, 2, 4), which fits into a concavity in the upper surface of the carina (*a'*, 3) immediately behind the swelling which contains the pollen. Close behind this the side of each ala bulges inwards, forming a depression, much broader and not less deep, which unites so firmly with a broad but shallow concavity in the upper surface of the carina (*b'*, 3) that it requires the greatest care to separate the two without tearing. This intimate union is due to the fact that the epidermis of the two petals over part of the surfaces of contact is composed of large hexagonal cells ( $\frac{1}{12}$  to  $\frac{1}{15}$  mm. in diameter) of which those on the one petal are strongly convex, and fit into corresponding concavities in the cells on the other. The same kind of union thus connects individual cells as on a larger scale connects the two petals.

The alæ and carina return after each depression to their former place. This is due: (1) to their own elasticity; (2) to the processes (*c*, 2, 4) which pass backwards and inwards from the superior basal angles of the alæ to lie upon the staminal column; (3) to the two superior basal lobes of the carina (*g*, *g*, 2, 3), which embrace the staminal column, and leave only a narrow slit between them in the middle line; (4) to the broad base of the vexillum, which curves round on each side so as to embrace completely the claws of the alæ and carina, while it in turn is embraced and held firmly in position by the calyx. By these four conditions all the parts of the flower are caused to return accurately to their former places after each insect-visit. The flowers therefore preserve the same appearance, and are visited repeatedly by insects, so that their pollen is carried away bit by bit, and the stigma at length rubbing on the under side of the insect becomes viscid (cf. *Lathyrus pratensis*) and covered with pollen brought from other flowers.

Though the parts of the flower close up firmly, their small size makes it easy for most bees to reach the honey. The abundance of honey and the aggregation of the flowers in handsome racemes lead to plentiful insect-visits.

**A. Hymenoptera—(a) Apidæ:** (1) *Apis mellifica*, L. ♀, exceedingly abundant. (It passes up the racemes, sucking for two to three seconds on each flower. When collecting pollen, it thrusts its head farther into the flower to depress the carina as much as possible; it takes at least six to eight seconds to brush off the pollen); (2) *Bombus agrorum*, F. ♀ ♀; (3) *B. hortorum*, L. ♀; (4) *B. Rajellus*, Ill. ♀; (5) *B. Scrimshiranus*, K. ♂ ♀ ♀; (6) *B. (Apathus) vestalis*, Fourc. ♂; (7) *Eucera longicornis*, L. ♀ ♂,—all only sucking. Various species with abdominal collecting-brushes, viz.: (8) *Megachile versicolor*, Sm. ♀; (9) *M. circumcincta*, K. ♀, ab.; (10) *M. maritima*, K. ♀; (11) *M. Willughbiella*,

honey legitimately on *V. sepium* from collecting pollen also on its flowers, and thus diminishes the number of their visits.

The stigma of *V. sepium* resembles that of *Lathyrus pratensis* in the way in which, when it is rubbed on a piece of glass, first its own pollen is rubbed off, and then its papillæ are injured and exude a sticky fluid.

The visitors are all bees, viz. :—(1) *Bombus agrorum*, F. ♀ ♂; (2) *B. Rajellus*, Ill. ♀; (3) *B. lapidarius*, L. ♀ ♂; (4) *B. silvarum*, L. ♀; (5) *Anthophora pilipes*, F. ♀ ♂,—all sucking normally; (6) *Bombus terrestris*, L. ♀, biting a hole and stealing the honey; (7) *Osmia rufa*, L. ♀; (8) *Apis mellifica*, L. ♀,—both make use of the holes made by *B. terrestris*. Both species have tongues long enough (*Osmia rufa* 8 mm., *Apis* 6 mm.), but are not strong enough to reach the honey in the legitimate way. See also No. 590, II.

*Vicia angustifolia*, Roth.—The brushes on the style are similar to those in *V. sepium*. The visitors are humble-bees, *Saropoda*, and *Lepidoptera* (590, II.).

119. *VICIA FABA*, L.—The brushes on the style are similar to those of *V. sepium*. In spite of the much greater size of the flower, both its honey and pollen are more accessible than those of *V. sepium*, though to reach the honey a longer proboscis is needed. The vexillum and alæ fit much less firmly together, and the carina is much more easily depressed. The thickened processes which in *V. sepium* project from the under side of the vexillum are here wanting; the claw of the vexillum (13 to 16 mm. long) is only loosely embraced by the calyx-tube, and for a distance of only 6 to 7 mm. above, and 8 to 10 mm. below. The vexillum is therefore easily pushed upwards, and those humble-bees which have a proboscis long enough to reach the honey in *V. Faba*, can do so more easily in that flower than in *V. sepium*. The two depressions by which the alæ and carina are united in *V. Cracca* and *V. sepium* occur also in the Bean, but in the latter the interlocking of the individual cells is less marked than in the others, so that the alæ and carina may be easily separated without tearing. The two posterior processes of the alæ, whose use is to keep the alæ and carina in their proper place in relation to the staminal column, are here much reduced and easily slip down from the upper surface of the carina. The alæ and carina are easily depressed, all the more that the alæ project far beyond the carina, forming a powerful lever acted on by the weight of the bee. Thus to reach the honey is here a matter of little difficulty, and is possible even for the smaller bees.

Owing to the small elasticity of the alæ and carina in the bean-flower, they fail to return to their former place if they are thrust far down, but leave the end of the style with its stigma and brushes and even the empty anthers exposed.

Visitors : A. Hymenoptera—*Apidæ* : (1) *Bombus hortorum*, L. ♀ (21) ; (2) *B. senilis*, Sm. ♀ (14—15) ; (3) *B. confusus*, Schenck, ♀ (14) ; (4) *B. lapidarius*, L. ♀ (12—14) ; (5) *B. silvarum*, L. ♀ (14),—all sucking in the normal way, ab. ; (6) *B. terrestris*, L. ♀ (7—9), sucking honey through holes bitten in the tube ; (7) *Apis mellifica*, L. ♀ (6), sometimes c.p., sometimes sucking through the holes bitten by *B. terrestris* ; in the former case it effects cross-fertilisation as well as those bees which suck in the normal manner ; (8) *Andrena convexiuscula*, K. ♀, c.p. ; (9) *A. labialis*, K. ♂, seeking in vain for honey ; (10) *Osmia rufa*, L. ♀, sucking normally,—it creeps so far into the flower that its whole head is hidden under the basal part of the vexillum. B. Coleoptera—*Malacodermata* : (11) *Malachius bipustulatus*, F., feeds upon the stamens after they have been laid bare by repeated visits of humble-bees.

Darwin found the fertility of the bean reduced to a third when insects were excluded by a net ; but if the flowers were shaken they produced good and well-filled pods though still protected from insects (152).

*Vicia amphicarpa*, Dorthes., has, besides its ordinary flowers, cleistogamic flowers without petals on subterranean shoots (399, 531).

120. *LATHYRUS PRATENSIS*, L.—This plant affords us another example of a papilionaceous flower, in which when the carina is depressed the tip of the style only emerges, and sweeps part of the pollen out of the apex of the carina by means of a brush, applying it to the under side of the bee, afterwards returning within the carina when the pressure is removed.

The style, which ascends vertically from the end of the horizontal ovary, curving slightly inwards, expands immediately below the oval stigma into an elliptic lamina. This lamina is covered, not only on the edges, as Delpino says (178), but on the whole surface turned towards the base of the flower, with hairs pointing obliquely upwards ; it lies in the conical apex of the carina, which points directly upwards (5, Fig. 70), and its hairy surface, turned towards the base of the flower, faces also the free edges of the tip of the carina. Between it and the margins of the carina is a deep pouch on each side (*p*, 5, 6), which is separated by a deep fold (*a'*) from the margin, and has its only entrance at the apex of the cone (*m*, 4, 5, 6). In the bud, this pouch contains all the anthers, which only dehisce immediately before or during the

expansion of the flower. The pouch becomes quite filled with pollen, and the anthers withdraw into its lower part. The hairy surface of the style and the stigma are thus covered with pollen in the opening flower, and each time that the carina is depressed they emerge at its apex sweeping a little pollen out. Since the hairs of the style do not pass into the lateral pouches, these would remain full of pollen, were it not that when the carina is depressed, the



FIG. 70. — *Lathyrus pratensis*, L.

- 1.—Flower, slightly enlarged, from the side.
- 2.—Ditto, from above, after removal of the calyx and vexillum ( $\times \frac{3}{4}$ ).
- 3.—Inner view of left ala.
- 4.—Flower, from above, after removal of vexillum and ala.
- 5.—Bud about to expand; the calyx, vexillum, and ala have been removed.
- 6.—Fore-part of ditto, from above.
- 7.—Style, from above.
- 8.—Ditto, from within.

a, slight concavity in the ala, which fits into the much deeper depression (a') in the carina; b, infolded process of the margin of the ala, pointing forwards and downwards, and fitting into the narrowest part of the depression in the carina; c, transverse depression in the ala, into which the ridge (o) of the vexillum fits; d, posterior alar process; e, claw of ala; f, incurved margin of ala; gg, edges of the carina; h, superior stamen; i, the coherent filaments; k k, the entrances to the honey; l, claw of carina; m, point where the stigma emerges when the carina is depressed; n, foliaceous expansion developed at the line of junction of the two carinal petals; o, ridge on the inferior surface of the vexillum, corresponding to a groove on its superior surface; p, bulge in the carina, beneath which are the anthers and style,—it is separated by a deep fold from the upper margin of the carina on each side.

empty anthers and the ends of the filaments pass into and push the pollen out of the pouches into the apex of the cone, whence it is swept out by the style. It requires considerable force to depress the carina, since the style with its hairs has at the same time to be forced through the slit at the apex of the carina.

It stands in close relation to this arrangement that the union of the two halves of the carina is strengthened by an anterior

membranous outgrowth (*n*, 4), and that the alæ and carina are connected very firmly with one another and with the staminal column. The union between the alæ and carina is formed in the following way:—The two folds or grooves, which in the erect extremity of the carina separate the two pouches from the free margins, are continued along the whole horizontal part of the carina near its upper border, and where the erect part joins the horizontal (at *a'*, 4, 5, 6) they each form a broad, rounded pit in which a fold of the ala (*a*, 1, 2, 3) lies; further towards the base of the flower they form a deep, narrow depression on each side of the cleft of the carina (*b'*, 4), in which a process directed downwards and forwards from the upper margin of the ala (*b'*, 2, 3) fits firmly. This interlocking is rendered more secure by the presence of numerous blunt projections on the marginal process of the ala (*b*), and in the full-grown flower it is difficult to separate the ala from the carina without tearing.

The union of the alæ and carina with the staminal column is effected, as in *Medicago sativa*, by two long, pouched processes of the alæ (directed backwards) which lie upon the column (*d*, 2, 3), meeting one another in the middle line. When the alæ and carina are depressed, these processes clasp the sides of the column, and as soon as the pressure is removed they return to their former place on its upper surface. The vexillum closes down firmly on the alæ, preventing useless insects, *e.g.* flies, from obtaining the honey which is secreted abundantly in the ordinary position and is reached by two unusually large openings. The vexillum, at the junction of its claw and lamina, bears two deep, narrow depressions which project below as two sharp ridges converging anteriorly (*o*, 1), and these fit firmly into two depressions in the alæ (*c*, 2, 3). Though the stigma is at first surrounded by the pollen of its own flower, it is probable that in case of insect-visits, cross-fertilisation is ensured. For this pollen with which the stigma is covered, is easily rubbed off if we draw the stigma over a glass plate; but immediately afterwards the stigmatic papillæ get rubbed away and leave a line of clear sticky fluid on the glass. Owing to the force which the mechanism of the flower renders necessary, the stigma must be rubbed hard on the under side of the bee, and thus without doubt, as Delpino supposes, its own pollen is rubbed off, its surface is rendered sticky by breaking down of the papillæ, and new pollen is made to adhere to it.

Whether in absence of insects the stigma finally becomes

viscid and capable of fecundation spontaneously, and is thus self-fertilised, is still undetermined.

The visitors are exclusively bees.

(1) *Eucera longicornis*, L. ♂, s., ab. ; (2) *Bombus agrorum*, F. ♀, s., freq. ; (3) *Diphysis serratulae*, Pz. ♀, s. ; (4) *Megachile maritima*, K. ♂, s. ; (5) *M. versicolor*, Sm. ♀, s. and c.p. (Brilon, 10 July, 1869.)

121. *LATHYRUS TUBEROSUS*, L.—I saw this plant visited very abundantly by the honey-bee in July 1868, in Thuringia. In sucking, the bee inserted its proboscis at one side, above one of the alæ. As it clung to one of the alæ and thrust its proboscis in laterally between the vexillum and carina, it pressed the carina so far down that the style and pollen emerged. In some cases the pollen did not come in contact with the bee, in others the stigma and the hairs of the style touched the bee on its side.

When collecting pollen, the bee clung to both alæ, thrusting its head and forelegs beneath the vexillum in the middle line. The stigma emerging from the carina came directly in contact with the under side of the bee, and cross-fertilisation was effected regularly. Besides the honey-bee I only saw two butterflies, a yellow *Hesperia*, and *Pieris rapæ*, L., sucking honey on the flowers.

122. *LATHYRUS SILVESTRIS*, L.—I saw this plant in Sauerland (July 12, 1869) visited also by hive-bees, both sucking and collecting pollen, and by numerous Lepidoptera, which however did not effect fertilisation (*Rhodocera rhamni*, L., *Pieris rapæ*, L., *Vanessa Io*, L., *V. urticae*, L., *Plusia gamma*, L.).

Delpino mentions as the chief fertiliser of this plant *Xylocopa violacea*, which does not occur in Westphalia, and justly emphasizes the slanting position of the style-brush as an adaptation rendering it easier for the bees to depress the carina (178).

Francis Darwin observed that bees rob *L. silvestris* of its honey by biting through the vexillum close above the calyx, and almost always just above the left honey-passage, which is commonly the larger,—a proof of capability to profit by experience. The unsymmetrical development of the passages leading to the honey in *L. silvestris* is in relation to the twisting of the style, and thus unsymmetrical development of the fruit seems related to both of these facts (169).

123. *LATHYRUS MONTANUS*, Bernh. (*Orobis tuberosus*, L.).—In Sauerland (July 1869) I saw this plant visited by *Eucera longicornis*,

L. ♀, s. and c.p; *Bombus pratorum*, L. ♀, s.; and *Hesperia silvanus*, Esp. s.

124. *LATHYRUS ODORATUS*, L., is visited by *Anthidium manicatum*, L. ♀, s.

125. *LATHYRUS VERNUS*, Bernh. (*Orobis vernus*, L.).—I have repeatedly found *Bombus hortorum*, L. ♀, sucking honey on this flower. A list of eleven other visitors, exclusively bees, is given in No. 590, II., p. 257.

*Lathyrus grandiflorus* is very rarely visited by bees in England. If the flowers are shaken they prove more fertile (152).

Delpino mentions the genera *Apis*, *Bombus*, *Frucera*, *Anthophora*, and *Xylocopa*, as the chief fertilisers of the various species of *Lathyrus* (178).

126. *PISUM SATIVUM*, L. (the Pea).—The mechanism of this flower agrees in most essential points with that of *Lathyrus pratensis*, but it has so many peculiarities that we must discuss it in almost complete detail.

The style ascends almost perpendicularly to the horizontal ovary, but its tip curves inwards so far that the stigma points almost horizontally towards the base of the flower (*st.* 7). The style is not swollen at the end, but is covered with long hairs on the side facing the base of the flower for over one-third of its length downwards from the stigma (7, 8, fig. 71). The style follows the line of union of the two halves of the carina, so the carina also is curved inwards in the shape of a sickle, and its conical tip, which incloses the brush upon the style, points towards the base of the flower (1, fig. 71). In this species also, as in *L. pratensis*, there is present in the bud on each side of the tip of the carina (*a*, 1, 4) a pouch, within which are the anthers; but the pouches are shallower and the folds separating them from the free margin are less marked, and the space in which the anthers lie in the bud is on the whole conical. The apex of the carina leaves, of course, an opening for the passage of the style (*o*, 4, 5). The anthers dehisce shortly before the bud expands; they fill the conical point of the carina with pollen and withdraw into the base of the cone, so that at the commencement of the flowering-period the stigma and the style-brush are covered with pollen, part of which is swept out at the apical orifice each time that the carina is depressed. The edges of the orifice yield to a pressure from within, but close

up again, so that while the stigma and style-brush return within the carina, great part of the pollen is swept off and remains outside. The ends of the filaments, lying in the base of the conical point of the carina, are slightly swollen even in the bud (7, fig. 71), but after the anthers have dehiscent they enlarge more (9), and so press the pollen forward more effectively than in the case of *Lathyrus pratensis*. They press the pollen in the base of

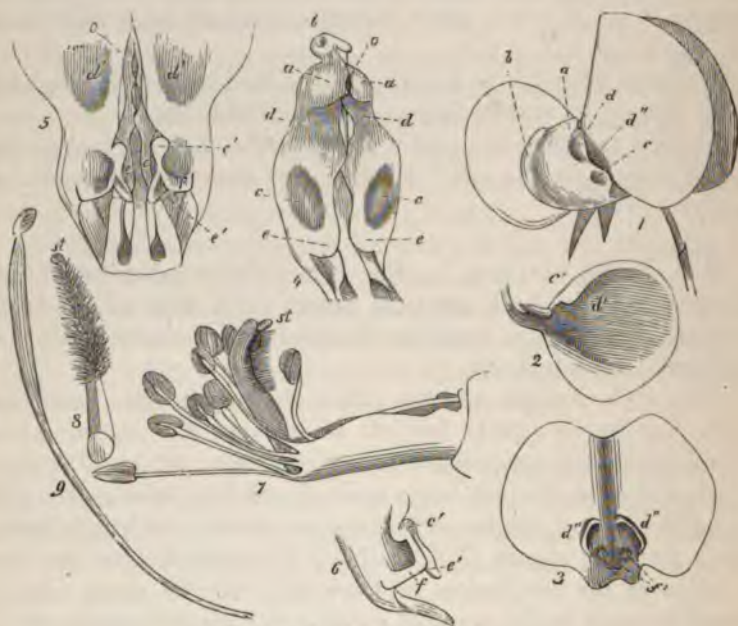


FIG. 71.—*Pisum sativum*, L.

- 1.—Flower, after removal of left ala.
- 2.—Inner view of left ala.
- 3.—Anterior view of vexillum.
- 4.—Carina, from above, enlarged.
- 5.—Ditto, inclosed by the ala.
- 6.—Basal half of left ala; outer view.
- 7.—Essential organs from a bud ( $\times 3\frac{1}{2}$ ).
- 8.—Anterior part of style, from within ( $\times 7$ ).
- 9.—One stamen of the flower.

(For letters, see the text.)

the cone forward to its apex, so that the style-brush on returning within the carina becomes covered again with pollen, and so a new portion of pollen is forced out at each depression of the carina. Thus the flower of the Pea combines the brush-mechanism with the piston-mechanism.

The force needed to depress the carina is both absolutely and relatively greater than in *Lathyrus pratensis*, since the style-brush

is curved more inwards, and the swollen ends of the filaments move with friction in the cone. On this account the union of the two carinal petals is strengthened by a still more marked outgrowth (*b*, 1, 4), and the alæ and carina are connected with each other and with the staminal column still more firmly. Each ala has at the base of its limb, close below its upper margin, a depression or invagination pointing forwards and downwards (*c*', 2, 5, 6), which is very firmly attached to a corresponding depression on the upper surface of the carinal petal (*c*, 1, 4); not only are the two pouches closely applied to one another throughout their whole extent, but over a great part of the surfaces in contact large hexagonal cells of the one petal project into hollows in corresponding cells on the other, so that it is scarcely possible to separate the petals from one another without tearing. Moreover, the anterior part of the ala is kept in a definite position relatively to the carina by a fold or groove (*d*', 2, 5) in its upper margin which fits into that groove (*d*) upon the carina which separates the pouch (*a*) from the edge. This second union of alæ and carina is strengthened by two deep and narrow depressions of the vexillum, which appear on its under side as hard, sharp ridges, converging anteriorly (*d*", 1, 3), and are received into the anterior alar grooves (*d*').

The position of the alæ and carina relatively to the staminal column is maintained very firmly and accurately. Each carinal petal possesses a lobe at its base (*e*, 4, 5), directed upwards and inwards, which lies upon the upper surface of the column and extends almost to the middle line. These two carinal lobes which embrace the column are pressed down and kept in their place by two processes of the alæ (*e*', 5, 6), directed inwards and backwards; the alar processes are themselves made secure by the vexillum, on whose broad, strong base two rounded swellings occur (*b*', 3) which rest upon two narrow surfaces of the alæ (*b*, 5, 6) passing horizontally backwards from the alar processes (*e*').

This firm union of the parts of the flower is of service to the plant in three ways. In the first place, it obliges an insect in search of honey, when standing on the alæ and thrusting its head beneath the vexillum, to use so much force in separating the alæ and vexillum that the brush and piston mechanism is set in action. Secondly, it ensures the perfect return of all the parts to their original position when the pressure is removed, and so causes the flower to retain its youthful appearance and to receive the repeated visits that its whole construction is designed for. Thirdly, it

excludes all insects from the honey which are not strong enough to perform the actions necessary for fertilisation.

Along with these obvious advantages, the firm closure of the flowers has the very important consequence that it makes the work difficult even for such bees as are able to reach the honey and to effect cross-fertilisation, and deters them from the plant when other more convenient flowers are at hand. In its original home the Pea no doubt adapted itself to some strong and at the same time diligent and skilful species of bee, which could easily depress the carina, and was plentiful enough in ordinary weather to act as the regular fertilising-agent. Under such conditions the advantages of firm closure would outweigh the disadvantages. In our climate, the Pea fails to find bees adapted for its flower, and it would be much better for it under these altered conditions to have its flowers less firmly shut. I have often watched beds of peas in bloom in my garden in sunny weather and have only occasionally seen a visitor, while beans, blooming at the same time in alternate beds, were abundantly visited by humble-bees.

The only insects which I have seen on the flowers in the course of four summers are : (1) *Eucera longicornis*, L. ; (2) *Megachile pyrina*, Lep. ;—the ♂ of both species, s. ; the ♀, s. and c.p. ; both freq., but not abundant ; (3) Two specimens of *Halictus sexnotatus*, K. ♀ ;—they collected pollen with difficulty, holding the edges of the carina apart anteriorly with their legs.

Though most flowers remain unvisited by insects, they all produce good fruit. The self-fertilisation which the structure of the flower necessitates must therefore be quite efficient ; and this indeed has been shown experimentally by Dr. Ogle, who found the Pea as productive when insects were excluded as when left unprotected (633).

#### Tribe *Phaseoleæ*.

*Amphicarpæa*, according to Torrey and Asa Gray (*N. Amer. Flora*, I., p. 291), has fertile cleistogamic flowers, and also flowers which open, but are for the most barren. Both kinds of flowers are above ground. Darwin found that subterranean pods of *Amphicarpæa monoica* which he received from Meehan, contained each a single seed, while the ordinary aerial pods, which he cultivated himself, contained from one to three small seeds ; these latter averaged only  $\frac{1}{8}$  of the weight of the subterranean seeds (167, 2nd Ed.).

The genera *Neurocarpum*, Desv., *Martiusia*, Schult., *Glycine*, L.,

*Galactia*, P. Br., and *Voandzeia*, Pet. Th., are stated by H. v. Mohl and Kuhn to possess cleistogamic flowers.

*Glycine chinensis*, Curt., is visited by bees only (590 II.).

*Centrosema virginiana* and *Clitoria mariana* both have their flowers inverted (729).

In *Erythrina crista-galli*, according to Delpino, the flower is inverted, the alæ are almost entirely aborted, and the carina forms a sheath covering the column and expanded below into a large honey-receptacle. Since the stigma somewhat overtops the anthers, the visitors, probably humming-birds, touch first the stigma then the anthers, and so effect cross-fertilisation. In *E. velutina* the flower is not inverted; the alæ and carina are reduced to minute rudiments, and the column lies fully exposed beneath the vexillum. The visitors, probably bees, must make their way between the column and the vexillum to reach the honey, which is secreted as in other Papilionaceæ, and so they come in contact with the stigma and anthers (178, 360). Belt (56) saw a species of *Erythrina* fertilised by humming-birds, which came in search of small insects that sucked honey in the flowers. Trelease saw *Erythrina herbacea* visited abundantly by ruby-throated humming-birds, and believes that the flower is adapted for cross-fertilisation by their agency (731).

Darwin states on the authority of MacArthur's observations that, in New South Wales, *Erythrina* does not produce good fruit unless the flowers are shaken (152).

PHASEOLUS.—The species of *Phaseolus* are distinguished from the other Papilionaceæ which have brush-hairs on the style by the helicoid twisting of the style and of the tip of the carina which incloses it; but here, as in the rest, when the carina is pressed down, the tip of the style issues with its stigma and pollen-brush, and these return within the carina when the pressure is removed. The twisting is towards the right in some species and towards the left in others, according to Delpino, and shows all stages from a mere sickle-shaped curvature (*P. angulosus*, etc.) to a helix of four to five coils (*P. Caracalla*), (172, 178).

The mechanism of the flower and the mode of fertilisation in the Scarlet Runner (*P. coccineus*, Lam.) have been thoroughly described by Mr. T. H. Farrer (240). The hive-bee and other small bees which are unable to press the carina down, obtain the honey by taking advantage of holes which a humble-bee (I suppose *B. terrestris*, L.) bites through the calyx. More powerful bees, with

sufficiently long proboscides, alight on the left ala, and in forcing the proboscis down into the flower bring its base in contact with the stigma.

Now, when the alæ and the carina (which is united to them) are further depressed, there emerges from the tubular apex of the carina, which is coiled nearly into two complete whorls, the similarly coiled style; and it emerges in such a way that its stigma points downwards and towards the left, and its pollen-covered hairs come in contact with the base of the insect's proboscis, dusting it with fresh pollen. In this manner is cross-fertilisation insured and self-fertilisation prevented in case of



FIG. 72. — *Phaseolus vulgaris*, L.

1.—Flower, viewed obliquely from above and in front.

2.—Pistil, enlarged.

a, calyx; b, vexillum; c c, alæ; d, apex of carina; e, ovary; f, style; g, its brush; h, stigma.

insect-visits; in absence of insects self-fertilisation cannot occur, since the stigma protrudes from the carina while the pollen is inclosed within it.

The similar mode of fertilisation in the Kidney Bean (*Phaseolus vulgaris*, L.) was described ten years earlier by Darwin (51), who showed by experiment that insect-visits are essential for the fertilisation of this plant. Plants covered with a fine net remained completely barren, unless the action of bees was artificially imitated. When Darwin repeated the experiment on a larger scale a few flowers on some specimens bore fruit; small insects (Thrips) had presumably gained access to these.<sup>1</sup>

<sup>1</sup> Dr. Ogle (No. 633) also gives a thorough description of the floral mechanism in *P. vulgaris* (French bean) and *P. coccinea* (Scarlet Runner). Of the flowers which Dr. Ogle protected from bees by means of a gauze net, no single one bore fruit.

Darwin had also shown that *cross-fertilisation* by insect-agency takes place to a large extent in *Phaseolus*. Mr. Coe planted four rows of Negro Dwarf Kidney Beans between some rows of white and brown Kidney Beans; near by were some Scarlet Runners. He let the black Kidney Beans run to seed, and over  $\frac{4}{5}$  of the beans produced showed all gradations from light brown to black, and some were mottled with white. Of the plants reared from these seeds every one differed from the rest in stature, leaves, colour and size of flower, time of flowering and of ripening fruit, size, form and colour of the pods; and the beans produced by them were of all shades between black and light-brown, some dark-purple, some slightly mottled, and of various shapes and sizes (151, 152).

In *P. multiflorus* the carina, with the inclosed style, are so bent that when the carina is depressed the style emerges pointing downwards and towards the left, so that a bee can only accomplish cross-fertilisation if it enters the flower to the left of the coil. Francis Darwin has pointed out that the tenth, free, stamen bears an appendage which prevents the bee from taking any other way towards the honey (169).

In regard to Treviranus' opinion that self-fertilisation is the general rule in Papilionaceæ, it is needless to discuss his arguments, since the only objection which he made to Darwin's experiments, viz. that the nets sheltered the plant from movements of the air (742) was experimentally refuted by Darwin. For the flowers in which Darwin imitated the action of the bees, though they grew beneath the net, were completely fertile.

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#### RETROSPECT OF PAPILIONACEÆ.

The Papilionaceæ which we have studied are all fertilised by bees, and in spite of their manifold peculiarities of detail they all agree in the following points regarding the arrangement and function of the parts of the flower:

The flowers stand more or less horizontal; except *Sarothamnus* they expose the stigma and pollen to contact only with the ventral surface of the bee, since the reproductive organs occupy the inferior side of the flower and are only curved upwards at the extremity. In the bud the reproductive organs are inclosed by the two inferior petals, these by the two lateral, and these again by the superior petal.

The two inferior petals cohere to form a "carina," which

incloses the reproductive organs and protects them from rain and from pollen-feeding insects. The two lateral petals (alæ) have a threefold function, serving (1) as a platform for bees to alight on; (2) as a lever to depress the carina; (3) to keep the carina in its place as regards the reproductive organs, and to bring it back to its place after depression if repeated insect-visits are necessary for fertilisation. In order to serve as levers for depressing the carina, the alæ must be united firmly therewith. This is either accomplished by certain areas of the alar laminæ bulging out and being received in hollows of the carina, or by interdigitation of processes on the contiguous surfaces of both; and such union is the firmer the more frequently the carina has to be depressed and again brought back to its original position in order to ensure cross-fertilisation.

The carina is mainly kept in its proper place and brought back to it after depression by basal lobes of the alæ which embrace the column; sometimes they form swollen pouches (*Trifolium*), sometimes they are produced into long processes (*Melilotus*, *Medicago*, etc.).

The vexillum, with its large, erect, coloured surface, is the chief agent in rendering the flower conspicuous; it also serves as a fixed point or fulcrum against which a bee may place its head while it pushes the carina with its feet resting upon the alæ.

The stigma and pollen must be applied to the ventral surface of the bee if cross-fertilisation is to result. The necessary arrangement is attained by the filaments cohering to form a cylinder round the pistil. In all Papilionaceæ which contain honey, the honey is secreted on the inner sides of the bases of the filaments, and it accumulates in the space between the stamens and pistil. Since the reproductive organs have to come in contact with the under side of the bee, it is clear that access to the honey must only be permitted above the reproductive organs. We find, accordingly, that in all Papilionaceæ which contain honey the coherent filaments leave a passage superiorly. One stamen here is separate from the rest and leaves two entrances to the honey free on either side of its base, either by curving upwards at its base, or by the neighbouring filaments curving outwards there, or in both modes combined.

The arrangement and action of the various parts of the flower in which all the Papilionaceæ (except *Onobrychis*) agree, cause the bees to act and move in a perfectly definite way, such as to ensure the stigma and pollen coming in contact with their under surfaces.

Four different types of structure may be distinguished in Papilionaceæ, according to the manner in which the pollen is applied to the bee. These distinctions were first drawn by Delpino (172, 178, 360), and transitions are not wanting from one to another :

1. Papilionaceæ in which the stamens and stigma emerge from the carina and again return within it. They admit repeated visits. (*Melilotus*, *Trifolium*, *Onobrychis*, *Cytisus*).

2. Papilionaceæ whose essential organs are confined under tension and explode (*Medicago*, *Genista*, *Sarothamnus*). In these only one insect's visit is effective, sometimes under certain conditions two (*Sarothamnus*).

3. Papilionaceæ with a piston-mechanism, which squeezes the pollen in small quantities out of the apex of the carina, and not only permits but requires numerous insect-visits. (*Lotus*, *Anthyllis*, *Ononis*, *Lupinus*).

4. Papilionaceæ with a brush of hairs upon the style which sweeps the pollen in small portions out of the apex of the carina. They for the most part require repeated insect-visits. (*Lathyrus*, *Pisum*, *Vicia*, *Phaseolus*).

In all these groups, the stigma and the pollen are applied to the under side of the bee. The pollen can therefore as a rule be collected quickest and most conveniently by bees with abdominal brushes ; and so we find *Lotus*, *Ononis*, and *Genista tinctoria* visited especially by these forms. In *Sarothamnus* both the upper and lower surfaces of the bee are dusted with pollen and come in contact with the stigma.

In those Papilionaceæ whose reproductive organs either simply emerge or spring out with an explosion, cross-fertilisation is ensured by the stigma projecting beyond the anthers, and coming first in contact with the bee. In those forms in which the pollen is squeezed or swept out bit by bit, the stigma is at first coated with its own pollen, which has probably no action upon the stigma and is rubbed away by the first visitors ; and the stigma only becomes adhesive and so capable of fertilisation after its papillæ have been exposed to friction. In absence of insects, self-fertilisation seems to take place on a large scale in very few Papilionaceæ (*Pisum*) ; in several it occurs to a small extent (*Trifolium repens*, *Vicia faba*) ; and in many it never occurs (*Phaseolus*, *Onobrychis*, *Sarothamnus*). In cases where self-fertilisation is impossible in the ordinary flowers, cleistogamic flowers which regularly fertilise themselves probably compensate.

Though almost exclusively adapted for fertilisation by bees, many Papilionaceæ allow their honey to be stolen by Lepidoptera and long-tongued flies (e.g. *Onobrychis*, *Lotus*, *Medicago falcata*). In others (e.g. *Vicia sepium*) the petals close up so firmly that only those bees which are in the habit of burrowing with all their strength, can force an entrance. Such forms as these exclude all visitors which would rob the flower of its honey without giving any return; but this advantage is more or less cancelled by the great diminution in the number of serviceable visitors.

*Trifolium pratense* excludes short-lipped bees from its honey by adhesion of the nine coherent filaments with the claws of the petals to form a long tube; the same end is attained in *Vicia faba* by the length of the claws of the petals and of the calyx-tube. Both plants are the more visited on this account by the hard-working humble-bees; but on the other hand they are liable to be often plundered by robber-bees which bite through the tube.

The great variety of arrangements in the various Papilionaceæ seems to be partly due to the manner in which every advantageous modification brings some disadvantage in its train; for in this way it is possible to have various combinations existing together, all perfectly adapted to the given conditions of life

#### CÆSALPINIACEÆ AND MIMOSACEÆ.

In these two families the essential organs are freely exposed. The petals or the stamens, or both together, attract insects. In *Mimosaceæ* the flowers are regular and united in capitula. In *Acacia Julibrissin* the central flower of the capitulum is transformed into a great nectary. In *Amherstia nobilis* the carina is abortive, and the alæ assume the function of rendering the flower conspicuous; the honey-receptacle is hollowed out into a long tube, which, together with the brilliant colour of the flowers, suggests humming-birds as the fertilisers (178, 360).

Fritz Müller found *Cassia multijuga* (Cæsalpiniaceæ) abundantly visited by bees (*Xylocopa*, *Centris*) in South Brazil. The pedicles were covered with larvæ of *Membracidae*, which secreted drops of honey at the posterior end of the abdomen, and this honey was sought by *Trigonia cacafo* (590, III.).

*Cassia* (?) is visited by humming-birds (*Mimus*) in Chili (Darwin, No. 164).

ORD. *ROSACEÆ*.Tribe *Prunæ*.

127. *PRUNUS COMMUNIS*, HUDS., *a*, (*P. spinosa*, L.), Blackthorn, Sloe.—When the flower opens the style stands some millimetres above the stamens, whose anthers are still closed, and which are bent down towards the centre of the flower. The stigma is already mature, and projects even from the half-open flower; insects, in alighting, come first in contact with it. In due course the petals spread out into a plane, and even further; the stamens become erect and incline outwards; the anthers dehisce, beginning with the outermost; the style also elongates, and overtops the shorter stamens immediately around it: its stigma is still fresh, and insect-visitors may therefore now lead to self-fertilisation. The flowers turn towards the sun, and in default of insect-visits self-fertilisation may take place by pollen falling on the stigma.

The numerous white flowers are very conspicuous on the black, still leafless twigs; their abundant honey attracts numerous insects, particularly flies and *Andrenæ*, all the more that the plant flowers early (April and beginning of May) in advance of most competitors.

Visitors: A. Hymenoptera—(*a*) *Apidæ*: (1) *Halictus cylindricus*, F. ♀, s. and c.p., ab.; (2) *H. albipes*, F. ♀, ditto; (3) *Andrena dorsata*, K. ♀, c.p.; (4) *A. parvula*, K. ♀, s. and c.p.; (5) *A. fasciata*, Wesm. ♂, s.; (6) *A. albicans*, K. ♀ ♂, c.p. and s.; (7) *A. fulva*, Schrank, ♀, s. and c.p.; (8) *A. fulvicrus*, K. ♀ ♂, s.; (9) *A. Gwynana*, K. ♀, s. and c.p.; (10) *A. rosæ*, Pz. ♀, s. and c.p.; (11) *A. Schrankella*, Nyl. ♀, c.p.; (12) *A. atriceps*, K. ♀ ♂, s.; (13) *Nomada succincta*, Pz. ♂, s.; (14) *Osmia rufa*, L. ♂, s.; (15) *Apis mellifica*, L. ♀, s. and c.p.; (*b*) *Tenthredinidæ*: (16) *Dolerus gonager*, Kl., s. B. Diptera—(*a*) *Empidæ*: (17) *Empis rustica*, Fall., s.; (*b*) *Syrphidæ*: (18) *Eristalis arbustorum*, L.; (19) *E. nemorum*, L.; (20) *E. intricarius*, L., all three s. and c.p.; (*c*) *Muscidæ*: (21) *Scatophaga stercoraria*, L.; (22) *S. merdaria*, F., both sucking; (23) *Chlorops*, s.; (24) *Sepsis*, s. ab.; (25) Species of *Anthomyia*, s.; (*d*) *Bibionidæ*: (26) *Bibio Marci*, L., l.h. C. Coleoptera—*Nitidulidæ*: (27) *Meligethes*, l.h. D. Lepidoptera—*Rhopalocera*: (28) *Vanessa Io*, L., s.

128. *PRUNUS PADUS*, L., Bird Cherry.—This species agrees on the whole in its proterogynous arrangement with *P. spinosa*, but the stamens remain throughout curved inwards, so that in the second stage insect visits may lead to self-fertilisation more readily than in the preceding species. In absence of insects, spontaneous self-fertilisation takes place regularly—since the inner stamens

dehisce while still bent down below the stigma, whose edge they come in contact with when they afterwards rise up.

Visitors: A. Diptera—*Empidæ*: (1) *Empis livida*, L. s.; (2) *E. rustica*, Fallen, s. Also numerous small gnats, licking honey. B. Hymenoptera—*Apidæ*: (3) *Andrena parvula*, K. ♀, s. C. Coleoptera—*Nitidulidæ*: (4) *Meligethes*, Lh. See also No. 590, II.

129. *PRUNUS DOMESTICA*, L., *P. AVIUM*, L., and *P. CERASUS*, L.—Anthers and stigmas ripen simultaneously, and spread apart out of the flower; the stigmas overtop the inner stamens but stand on a level with the outer ones. Cross-fertilisation is favoured by the likelihood of insects touching the stigma and anthers with different parts of their bodies while sucking the honey secreted by the receptacular tube. Insects collecting or feeding on pollen must lead to self-fertilisation and cross-fertilisation indiscriminately. In flowers obliquely placed, pollen may readily fall from the taller anthers upon the stigma.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, s., very ab.; (2) *Bombus lapidarius*, L. ♀; (3) *B. terrestris*, L. ♀; (4) *B. hortorum*, L. ♀, all three sucking; (5) *Osmia rufa*, L. ♀ ♂, s., ab.; (6) *O. cornuta*, Latr. ♀ ♂, s.; (7) *Andrena fulva*, Schr. ♀, s. and c.p.; (8) *A. albicans*, K. ♀ ♂, c.p. and s.; very ab. B. Diptera—*Syrphidæ*: (9) *Rhingia rostrata*, L., s., ab.; (10) *Eristalis tenax*, L.; (11) *E. arbustorum*, L., s. C. Lepidoptera—*Rhopalocera*: (12) *Pieris brassicæ*, L.; (13) *P. rapæ*, L.; (14) *P. napi*, L., all three sucking. See also No. 590, II.

#### Tribe *Spirææ*.

130. *SPIRÆA ULMARIA*, L.—The flowers contain no honey but a great quantity of pollen. The stamens at first arch over towards the middle of the flower, so as to cover the stigmas completely; they gradually become erect and incline outwards in centripetal succession, and the anthers then dehisce, covering themselves all round with pollen. When the stamens have risen up, the centre of the flower becomes the most convenient place both for small insects to settle on, and for larger insects traversing the inflorescence to step upon. Cross-fertilisation is thus readily performed, but self-fertilisation is also very liable to occur.

The crowded inflorescences not only attract numerous insects but also lead to great economy of time in the process of fertilisation. In the absence of insects, self-fertilisation almost always takes

place, and cross-fertilisation may also occur by the outer stamens of one flower coming to stand over the stigmas of the next.

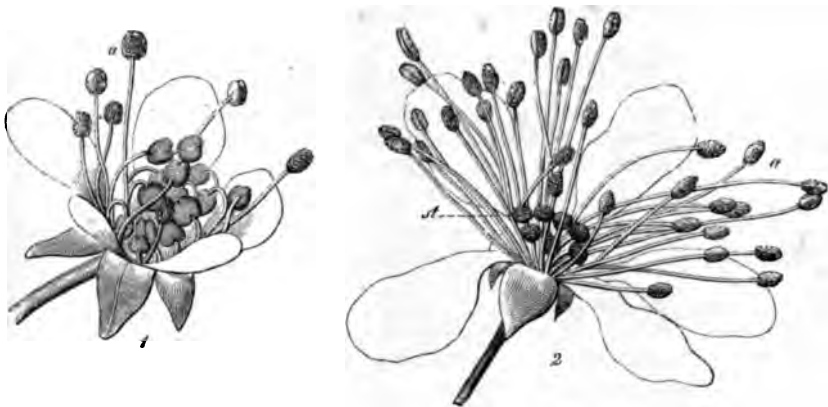


FIG. 73.—*Spiraea ulmaria*, L.

1.—Young flower.  
2.—Older ditto.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, ab., c.p.; (2) *Andrena Coitana*, K. ♀, c.p.; (3) *Prosopis communis*, Nyl. ♀, f.p.; (b) *Chrysidæ*: (4) *Chrysis ignita*, L.; (5) *Elampus auratus*, Wesm.; (6) *Hedychrum lucidulum*, F. (I have never seen *Chrysidæ* eating pollen, and so I suppose that these species were attracted by the flowers without finding anything useful in them). B. Diptera—(a) *Syrphidæ*: (7) *Eristalis horticola*, Deg. (Sld.); (8) *E. arbustorum*, L.; (9) *E. nemorum*, L.; (10) *E. tenax*, L.; (11) *E. sepulcralis*, L.,—all eating pollen, in great numbers; (12) *Volucella bombylans*, L.; (13) *Helophilus florens*, L.; (14) *Syritta pipiens*, L., all f.p.; (b) *Muscidæ*: (15) *Anthomyia* sp. C. Coleoptera—(a) *Nitidulidæ*: (16) *Cychramus luteus*, F.; (b) *Dermestidæ*: (17) *Anthrenus pimpinellæ*, F.; (c) *Lamellicornia*: (18) *Trichius fasciatus*, L.; (19) *Cetonia aurata*, L.,—both feeding on the tissues of the flower; (d) *Mordellidæ*: (20) *Mordella aculeata*, L.; (e) *Cerambycidæ*: (21) *Pachyta 8-maculata*, F. (Sld.); (22) *Strangalia attenuata*, L.,—both feeding on the anthers.

131. *SPIRÆA FILIPENDULA*, L.—The flowers secrete no honey, and are, therefore, visited only by pollen-seeking insects, which, owing to the position of the parts, usually alight on the stigmas and perform cross-fertilisation. The petals are bent backwards and downwards when the flower is fully expanded, and they are attached by such narrow claws that they dip down under the weight of a small bee or fly, and are, therefore, unsuitable for a standing-place. The stamens before dehiscing are bent far outwards, and in the centre of the flower nine to twelve broad bifid styles spread out into

a horizontal plane, forming a disc round whose edge the stigmas, directed outwards and upwards, stand. In absence of insects, self-fertilisation may readily take place, since the innermost stamens often remain directed inwards until dehiscence has taken place.

Visitors: A. Hymenoptera—*Apidae*: (1) *Haliectus zonulus*, Sm., ♀, c.p.; (2) *H. sexnotatus*, K., ♀, c.p. B. Diptera—*Syrphidae*: (3) *Eristalis arbutorum*, L.; (4) *E. nemorum*, L.; (5) *Helophilus florens*, L.; (6) *Syritta pipiens*, L.—all eating pollen. C. Coleoptera—*Lamellicornia*: (7) *Trichius fasciatus*, L., rapidly devouring the anthers.

132. *SPIRÆA ARUNCUS*, L.—The flowers of this species also are devoid of honey.

Visitors (in my garden at Lippstadt): A. Hymenoptera—(a) *Apidae*: (1) *Prosopis signata*, Pz. ♀ ♂, f.p.; (b) *Sphegidae*: (2) *Oxybelus bellus*, Dlb., f.p.; (c) *Vespidae*: (3) *Odynerus sinuatus*, F., seeking vainly for honey. B. Diptera—(a) *Syrphidae*: (4) *Syritta pipiens*, L., f.p., very ab.; (b) *Muscidae*: (5) Species of *Anthomyia*, f.p. C. Coleoptera—(a) *Nitidulidae*: (6) *Meligethes*, ab.; (b) *Dermeatidae*: (7) *Anthrenus Scrophulariæ*, L., not rare; (8) *A. pimpinellæ*, F., very ab.; (9) *A. claviger*, L., scarce.

133. *SPIRÆA SALICIFOLIA*, L., *S. ULMIFOLIA*, L., *S. SORBIFOLIA*, L.—These commonly cultivated species secure very numerous insect-visits by their densely crowded inflorescences and their abundant pollen and honey. The distinctly proterogynous condition of the flowers favours cross-fertilisation to a great extent, but self-fertilisation is also provided for in case of continuous wet weather. An annular, orange-coloured disk in the base of the receptacular tube, internal to the insertion of the stamens, secretes abundant honey in the form of small drops. In *S. salicifolia*, this disk has ten notches.

Already before the flower opens, the broad stigmas are provided with papillæ and overtop the incurved stamens. When the flower expands, the stamens gradually rise up, and, one by one, beginning with the outermost, their anthers dehisce, coating themselves all round with pollen. The stigmas still remain fresh, and thus, though at first only cross-fertilisation is possible, later on self-fertilisation also may take place.

The three species grow with us in the same localities and in nearly equal abundance. They are visited by the same insects, and I have grouped the visitors in a single list.

A. Diptera—(a) *Stratiomyidae*: (1) *Stratiomys riparia*, Mgn., s.; (b) *Empidæ*: (2) *Empis opaca*, F., ab.; (3) *E. tessellata*, F., very ab.; (4) *E.*

punctata, F., all three sucking ; (c) *Syrphidæ* : (5) *Chrysotoxum festivum*, L. ; (6) *Pipiza funebris*, Mgn. ; (7) *Chrysogaster viduata*, L. ; (8) *Syrphus ribesii*, L., f.p. ; (9) *S. excisus*, Zett. ; (10) *Melithreptus strigatus*, Stæg. ; (11) *Ascia podagrica*, F., s. ; (12) *A. lanceolata*, Mgn., do. ; (13) *Rhingia rostrata*, L., s.,

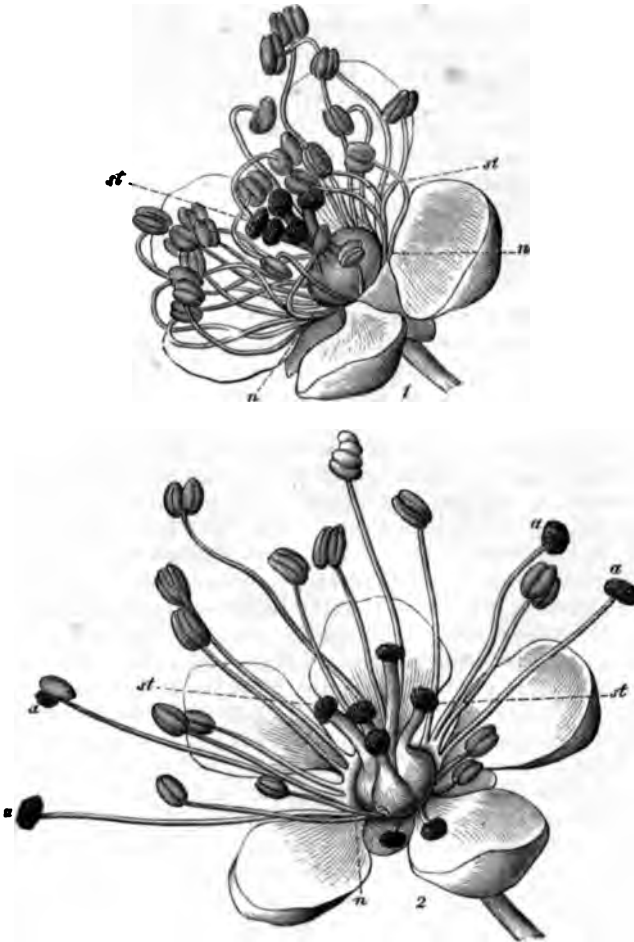


FIG. 74.—*Spiraea sorbifolia*, L.

1.—Young flower.

2.—Older ditto, whose anthers (a) have in part dehisced.

n, nectary ; st, stigma ; a, dehiscent anther.

very ab. ; (14) *Volucella plumata*, Mgn. ; (15) *Eristalis arbustorum*, L. ; (16) *E. nemorum*, L. ; (17) *E. sepulcralis*, L. ; (18) *E. tenax*, L. ; (19) *E. pertinax*, Scop. ; (20) *E. intricarius*, L., all both s. and f.p., very ab. ; (21) *Helophilus floreus*, L., s., freq. ; (22) *Xylota ignava*, Pz. ; (23) *X. segnis*, Pz. ; (24) *X.*

lenta, Pz. ; (25) *Syricta pipiens*, L., s. and f.p., very ab. ; (d) *Conopidae* : (26) *Physocephala rufipes*, F., s. ; (27) *Myopa polystigma*, Rondani, s. ; (e) *Muscidae* : (28) *Gymnosoma rotundata*, L. ; (29) *Echinomyia fera*, L. ; (30) *E. magnicornis*, Zett. (Tekl. B.) ; (31) *Sarcophaga carnaria*, L., s. ; (32) *S. albiceps*, Mgn., do. ; (33) *Onesia cognata*, Mgn. ; (34) *O. floralis*, R. D. (both identified by Herr Winnertz) ; (35) *Mesembrina meridiana*, L. ; (36) *Lucilia cornicina*, F., s. ; (37) *L. silvarum*, Mgn., s. ; (38) *Musca corvina*, F. ; (39) *Cytoneura simplex*, Læw. (identified by Herr Winnertz) ; (40) species of *Anthomyia* ; (f) *Bibionidae* : (41) *Bibio hortulanus*, L., l.h. ; (g) *Tipulidae* : (42) *Pachyrrhina pratensis*, L., do. ; (h) *Chironomidae* : (43) *Ceratopogon*, very ab., s. B. Hymenoptera—(a) *Tenthredinidae* : (44) *Tenthredo bicincta*, L., l.h. ; (b) *Ichneumonidae* : (45) Various ; (c) *Formicidae* : (46) Many small ants lick the honey, and also capture the numerous small midges which are attracted by it ; (d) *Chrysidæ* : (47) *Hedychrum lucidulum*, F. ♂ ; (e) *Sphegidae* : (48) *Oxybelus uniglumis*, L., very ab., s. ; (49) *O. bellus*, Dlb., do. ; (50) *Crabro lapidarius*, Pz. ♂, s. ; (51) *Psen atratus*, Pz., s. ; (52) *Passalæus monilicornis*, Dlb. ♀, s. ; (53) *Cerceris arenaria*, L., not rare ; (54) *Ammophila sabulosa*, L. ; (55) *Pompilus neglectus*, Wesm., s. ; (f) *Vespidae* : (56) *Odynerus quinquefasciatus*, F. ; (g) *Apidae* : (57) *Halictus sexstrigatus*, Schenck, ♀, s. ; (58) *H. sexnotatus*, K. ♀, c.p. ; (59) *H. flavipes*, K. ♀ ; (60) *Andrena albicans*, K. ♀ ♂, c.p. and s., ab. ; (61) *A. fucata*, Sm. ♀, s. and c.p. ; (62) *A. Schrankella*, Nyl. ♂, s. ; (63) *A. fulvicrus*, K. ♂, s. ; (64) *A. parvula*, K. ♀, s. and c.p., ab. ; (65) *A. dorsata*, K. ♀, s. and c.p., very ab. ; (66) *A. albicans*, K. ♀, s. and c.p., ab. ; (67) *A. nigroænea*, K. ♂, s. ; (68) *A. Trimmerana*, K. ♀, s. ; (69) *Osmia rufa*, L. ♀, c.p. ; (70) *Bombus terrestris*, L. ♀, c.p. and s. ; (71) *B. senilis*, Sm. ♀, c.p. ; (72) *B. Scrimshiranus*, K. ♀, c.p. ; (73) *Apis mellifica*, L. ♀, c.p. and s. C. Coleoptera—(a) *Dermestidae* : (74) *Anthrenus scrophulariæ*, L. ; (75) *A. pimpinellæ*, F. ; (76) *A. muscorum*, L. ; (77) *Attagenus pelli*, L. ; (78) *Byturus fumatus*, L., all five very ab., l.h. ; (b) *Nitidulidae* : (79) *Meligethes*, ab. ; (c) *Elateridae* : (80) *Lacon murinus*, L. ; (81) *Cardiophorus cinereus*, Hbst., l.h. ; (d) *Lamellicornia* : (82) *Trichius fasciatus*, L. ; (83) *Phyllopertha horticola*, L., both feeding on the tissues of the flower ; (e) *Malacodermata* : (84) *Malachius bipustulatus*, F., devouring the anthers ; (85) *Dasytes flavipes*, L. ; (f) *Mordellidae* : (86) *Anaspis frontalis*, L., ab. ; (87) *A. maculata*, Fourc., both l.h. ; (g) *Cerambycidae* : (88) *Clytus arietis*, L., l.h. ; (89) *Strangalia nigra*, L. ; (90) *Str. attenuata*, L., freq. ; (91) *S. armata*, Hbst. ; (92) *Leptura livida*, F., very ab. ; (93) *Grammoptera ruficornis*, F., all l.h. ; (h) *Cistelidae* : (94) *Cistela murina*, L., ab., feeding on the anthers and other tissues. D. Neuroptera—(95) *Panorpa communis*, L., l.h. ; (96) *Agrion*, flew not infrequently on to flowers of *Spiræa* but apparently only to sun itself (June 4, 1870). E. Lepidoptera—(97) *Tortrix plumbagana*, Tr. ; (98) *Adela sulzella*, W. V., ab., s. (both identified by Dr. Speyer). See also No. 590, II.

#### Tribe Rubeeæ.

134. *RUBUS IDÆUS*, L. (Raspberry).—In the Raspberry and Blackberry honey is abundantly secreted by a fleshy ring or disk upon the border of the receptacular tube, internal to the attachment of the stamens. In the Raspberry the small narrow petals remain

erect, and even inclined towards one another above, and the stamens, which dehisce either on the side towards, or on that away from, the centre, have no room to spread out, but remain closely packed between the styles and petals; so that an insect may easily insert its proboscis, but scarcely its whole head, between the styles and stamens to reach the honey-secreting ring. The accessibility of the honey is thus greatly reduced, but at the same time, since part of the stigmas come in contact with the anthers, self-fertilisation is insured. In the event of insect-visits cross-fertilisation is easily accomplished; for the insect often alights in the centre of the flower, touching the stigmas first, and in bending the head down between stigmas and stamens the former may easily be dusted with pollen from another flower. The much less conspicuous flowers and less accessible honey cause insect-visits to be fewer and less varied than in the case of the bramble; and self-fertilisation is very frequently made use of.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, very ab., both s. and c.p.; (2) *Bombus agrorum*, F. ♀, s., ab.; (3) *B. pratorum*, L. ♀ ♂, s. and c.p., freq.; (4) *B. hortorum*, L. ♀, c.p.; (5) *B. senilis*, Sm. ♀, s.; (6) *B. silvarum*, L. ♀, s.; (7) *Andrena nigroarnea*, K. ♂, s.; (8) *A. albicus*, K. ♂, s.; (9) *Halictus sexnotatus*, K. ♀; (10) *H. lucidus*, Schenck, ♀; (11) *H. nitidusculus*, K. ♀, all three sucking; (b) *Sphegidae*: (12) *Gorytes mystaceus*, L.; (c) *Tenthredinidae*: (13) *Tenthredo rustica*, L. B. Diptera—*Syrphidae*: (14) *Rhingia rostrata*, L., s. and f.p.; (15) *Volucella pellucens*, L. (Sld.), s. and f.p. C. Coleoptera—(a) *Dermestidae*: (16) *Byturus fumatus*, L., devouring the anthers and licking honey; (b) *Cerambycidae*: (17) *Pachyta 8-maculata*, F., licking honey and feeding on the tissues of the flower, ab. in Sld.

135. *RUBUS FRUTICOSUS*, L. (Blackberry, Bramble).—The flowers of the bramble have advantages in several respects over those of the Raspberry; the large petals, spreading out flat, are very conspicuous; and the stamens also spreading outwards leave the honey-secreting ring easily accessible. These two characters induce much more numerous and varied insect-visits than the Raspberry obtains. The outermost anthers are the first to dehisce, and the stigmas ripen at the same time; and most flowers have been cross-fertilised before the inner anthers are mature. Insects may alight with equal convenience either in the centre or at the circumference of the flower, and therefore come in contact either with the stigmas or with the ripe stamens. Only the innermost stamens rise up after they have dehisced, to come in contact with the outermost stigmas.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, c.p. and s., very ab.; (2) *Bombus agrorum*, F. ♀; (3) *B. terrestris*, L. ♀; (4) *B. hortorum*, L. ♀; (5) *B. pratorum*, L. ♂♂; (6) *B. Scrimshirani*, K. ♀; (7) *B. silvarum*, L. ♀, all these humble-bees sometimes suck, sometimes collect pollen, while the following parasitic humble-bees of course only suck; (8) *B. (Apathus) vestalis*, Fourc. ♀; (9) *B. campestris*, Pz. ♀; (10) *Macropis labiata*, Pz. ♂; (11) *Andrena Gwynana*, K. ♀; (12) *A. albicus*, K. ♂; (13) *A. thoracica*, K. ♀; (14) *Halictus zonulus*, Sm. ♀; (15) *H. lucidulus*, Schenck, ♀; (16) *H. villosulus*, K. ♀; (17) *H. sexnotatus*, K. ♀; (18) *H. cylindricus*, F. ♂♂; (10)—(18) all sucking; (19) *H. leucozonius*, K. ♀, c.p.; (20) *H. albipes*, F. ♀, c.p.; (21) *Celiomyia umbrina*, Sm. ♀♂; (22) *Nomada ruficornis*, L. ♂; (23) *N. lineola*, Pz. ♂; (24) *N. lateralis*, Pz. ♀; (25) *N. Fabriciana*, L. ♀; (26) *Diphysis serratulæ*, Pz. ♀; (27) *Osmia fusca*, Christ. ♀; (28) *Stelis breviscula*, Nyl. ♂; (29) *Prosopis excisa*, Schenck, ♂; (30) *P. variegata*, F. ♂; (31) *P. communis*, Nyl. ♂, all sucking; (b) *Sphegidae*: (32) *Crabro patellatus*, v. d. L. ♀♂; (33) *Oxybelus uniglumis*, L. ♀♂; (34) *Ammophila sabulosa*, L. ♀♂; (35) *A. (Miscus) campestris*, Jur. ♂; (36) *Cerceris nasuta*, Dlb. ♂, all sucking. B. Diptera—(a) *Stratiomyidae*: (37) *Sargus cuprarius*, L., s.; (38) *Chrysomyia formosa*, Scop. s.; (b) *Empidae*: (39) *Empis livida*, L., ab.; (40) *E. tessellata*, F., both sucking; (c) *Syrphidae*: (41) *Ascia podagrica*, F.; (42) *Syrpitta pipiens*, L., ab.; (43) *Eristalis tenax*, L., ab.; (43b) *Helophilus pendulus*, L., ab.; (44) *Chrysotoxum arcuatum*, L. (Sld.); (45) *Volucella pellucens*, L. (Sld.); (46) *Rhingia rostrata*, L., all sometimes sucking, sometimes collecting pollen; (d) *Conopidae*: (47) *Physocephala rufipes*, F., s.; (e) *Tipulidae*: (48) *Tipula oleracea*, L., s. C. Coleoptera—(a) *Dermestidae*: (49) *Byturus fumatus*, L., s. and feeding on the tissues of the flower; (b) *Elateridae*: (50) *Diacanthus æneus*, L.; (51) *Limonium cylindricus*, Payk., both feeding on the softer tissues; (c) *Lamellicornia*: (52) *Trichius fasciatus*, L., do.; (d) *Malacodermata*: (53) *Telephorus rusticus*, L., (54) *Malachius bipustulatus*, F., do.; (e) *Ædemeridae*: (55) *Ædemera virescens*, L., do., and licking honey; (f) *Cerambycidae*: (56) *Clytus arietis*, L.; (57) *Leptura livida*, F.; (58) *Pachyta 8-maculata*, F. (Sld., ab.); (59) *Strangalia armata*, Hbst.; (60) *S. atra*, F.; (61) *S. nigra*, L.; (62) *S. melanura*, L., all sometimes licking honey, sometimes feeding on pollen, anthers, and other parts of the flower; (g) *Nitidulidae*: (63) *Meligethes*, ab. D. Lepidoptera—*Rhopalocera*: (64) *Argynnis Paphia*, L.; (65) *Pieris cratægi*, L.; (66) *P. napi*, L.; (67) *Hesperia paniscus*, F., all sucking. Twenty-six additional visitors are enumerated in No. 590. II.

*Rubus saxatilis*, L., is proterogynous, with long-lived stigmas. Its arrangements for cross-fertilisation resemble those of *Cotoneaster*. The fertilising agents are chiefly bees (609, fig. 85).

#### Tribe *Potentilleæ*.

*Dryas octopetala*, L., is androdicæous. Its hermaphrodite flowers are usually feebly proterogynous, after the manner of *Geum urbanum*, L.; but sometimes the stigmas are covered over by the

inner stamens even for some time after the outer anthers have dehisced, and such flowers therefore are essentially proterandrous (609).

136. *GEUM RIVALE*, L.—The honey exudes in numerous minute drops from the base of the receptacular tube, and is diligently sought by humble-bees while most of the flowers are still in the bud. *Bombus terrestris*, L. ♀, which steals honey from many different flowers, sucks honey in *Geum rivale* also from the outside in yet unopened flowers, thrusting in its proboscis between the sepals and petals. Even after the flower is expanded, *B. terrestris* often, and other species of *Bombus* occasionally, obtain the honey in this way; but for the most part humble-bees hang suspended to the flower, which they grasp with their mid and hindlegs, putting their forelegs and head inside the flower. The outer portion of the honey they seem to reach more easily from the outside. This liability of the honey to be reached from the outside is a serious imperfection in the flower, which thus gets deprived of its honey without receiving cross-fertilisation in return.

The flowers are proterogynous, and in young flowers the ripe stigmas project far beyond the still closed anthers. Cross-fertilisation is thus insured if at this time a bee inserts its head in the legitimate manner. Later, the stamens elongate till their anthers stand on a level with the outermost stigmas; in dehiscence, the anthers cover themselves all round with pollen. When the flower closes, the anthers are brought in contact with the outermost stigmas, and self-fertilisation results, unless the pollen has been removed by bees. Since the plant grows sheltered in woods, it is visited by numerous bees even in unfavourable weather.

According to Mr. T. Whitelegge, *G. rivale* is occasionally andromœcious (774).

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus terrestris*, L. ♀; (2) *B. lapidarius*, L. ♀; (3) *B. confusus*, Schenck, ♀; (4) *B. hypnorum*, L. ♀; (5) *B. pratorum*, L. ♀ ♂; (6) *B. Scrimshirani*, L. ♀ ♂; (7) *B. hortorum*, L. ♀ ♂, very ab.; (8) *B. agrorum*, F. ♀; (9) *B. fragrans*, K. ♀, very scarce; (10) *B. senilis*, Smith, ♀; (11) *B. silvarum*, L. ♀, ab., all sucking (*B. silvarum*, ♀, and *B. pratorum*, ♂, also collected pollen, hanging back downwards to the flower); (12) *Apis mellifica*, L. ♂, sucking the flowers from outside, ab.; (13) *Andrena helvola*, L. ♀, seeking vainly for honey. B. Diptera—*Syrphidae*: (14) *Rhingia rostrata*, L., very ab., s. and f.p. C. Coleoptera—*Nitidulidae*: (15) *Meligethes*, ab.

*Geum reptans*, L., and *G. montanum*, L., are proterogynous and androdicœcious; that is to say, besides the ordinary individuals

with hermaphrodite proterogynous flowers, other plants occur in all of whose flowers the pistil is suppressed while the stamens remain (609).

137. *GEUM URBANUM*, L.—The flowers are much smaller than those of *G. rivale*, and appear at a season (July, August) and in spots where many more conspicuous flowers compete with them. They accordingly receive few insect-visits, and rely for the most part on self-fertilisation.

Honey is secreted by a green, fleshy, annular ridge at the base of the receptacular tube, internal to the insertion of the stamens. When the flower opens all the stamens are bent inwards, so that their anthers lie close upon the outer carpels, while the inner styles with ripe stigmas project in the centre of the flower. The outermost stamens now bend outwards and the anthers dehisce, turning their pollen-covered surfaces upwards; when the innermost stamens dehisce in their turn, some of their pollen almost always comes upon the outer stigmas. If the flower is visited early by insects, its feebly-marked proterogynous dichogamy may insure cross-fertilisation; if the visits are deferred till later, crossing may still be effected by an insect which alights, dusted with pollen, in the centre of the flower. But self-fertilisation must take place very often, both spontaneously and by the agency of insects which alight at the edge of the flower.

I have only observed the following visitors: A. Diptera—*Syrphidæ*: (1) *Melithreptus scriptus*, L., s. and f.p. B. Coleoptera—*Dermestidæ*: (2) *Byturus fumatus*, L., f.p.

138. *FRAGARIA VESCA*, L. (Strawberry).—The honey is secreted by a narrow, fleshy ring at the base of the receptacular tube, sheltered between the stamens and the outer carpels. The petals spread out into a level disk, forming a convenient alighting-place for insects. An insect standing on a petal must, to reach the honey, thrust its head between the stamens, and bring it in contact with the stigmas. If both stigmas and anthers ripened together self-fertilisation would thus be occasioned directly by the insects, but as a matter of fact the stamens come to maturity much later than the stigmas. Cross-fertilisation is also favoured by the shape and manner of dehiscence of the anthers; for these are expanded into flat disks, so that the intervening spaces are so much narrowed that even *Halictus* and the smaller flies cannot reach the nectary with their heads, without rubbing against some of the anthers. The

anthers dehisce at their edges, and are only covered with pollen at these parts. In absence of insects, I have noticed, in the case of plants blooming in my room, that some pollen falls at length upon the stigmas, in consequence of the oblique (light-seeking) position of the flower.

Visitors: A. Diptera—(a) *Empidæ*: (1) *Empis livida*, L., s.; (b) *Syrphidæ*: (2) *Eristalis sepulcralis*, L., s.; (3) *Syrphus*, s.; (4) *Melithreptus menthastri*, L., s.; (5) *Rhingia rostrata*, L., s.; (6) *Syritta pipiens*, L., s., ab.; (c) *Muscidæ*: (7) *Anthomyia* sp.; (8) *Musca corvina*, F. B. Coleoptera—(a) *Dermetidæ*: (9) *Anthrenus pimpinellæ*, F., l.h.; (10) *A. scrophulariæ*, L., l.h.; (b) *Nitidulidæ*: (11) *Meligethes*, ab.; (c) *Malacodermata*: (12) *Dasytes flavipes*, F.; (13) *Malachius bipustulatus*, F., both species licking honey, and also devouring the anthers; (d) *Mordellidæ*: (14) *Mordella aculeata*, L., l.h.; (e) *Cerambycidæ*: (15) *Grammoptera ruficornis*, Pz., not rare, l.h., and also devouring the anthers. C. Thysanoptera—(16) *Thrips*, ab., s. D. Hymenoptera—(a) *Apidæ*: (17) *Prosopis communis*, Nyl. ♀; (18) *Halictus lucidulus*, Schenck, ♀, s.; (19) *H. sexstrigatus*, Schenck, ♀; (20) *Andrena dorsata*, K. ♀, c.p.; (21) *Nomada sexfasciatus*, Pz. ♂; (22) *N. ruficornis*, L. ♀, s.; (23) *N. signata*, Jur. ♂, s.; (24) *Apis mellifica*, L. ♀, c.p.; (b) *Sphegidæ*: (25) *Oxybelus uniglutinis*, L., l.h. See also No. 590, II, and No. 609.

In the United States, cultivated species of *Fragaria* incline to diœcism.

139. *POTENTILLA VERNA*, L.—The annular ridge on the inner wall of the receptacular tube, which surrounds the base of the stamens and is marked by its dark, sometimes reddish-yellow, colour, and bright polished appearance, secretes honey not in drops but in a very evident smooth adherent layer. The anthers get covered on both sides with pollen, and ripen simultaneously with the stigmas. Insect-visitors alight sometimes in the middle of the flower, sometimes on the petals; in the latter case they dust themselves with pollen, but are not likely to come in contact at all with the stigmas, as the honey-secreting ring lies farther outwards than in the preceding species; if they alight in the middle of the next flower, cross-fertilisation is accomplished. Self-fertilisation must in any case be a frequent occurrence. In dull weather the flowers close partially, and at night they shut completely, bringing the anthers in contact with the stigmas.

Visitors (from April 21 to May 24): A. Hymenoptera—*Apidæ*: (1) *Halictus leucopus*, K. ♀, s. and c.p.; (2) *H. flavipes*, K. ♀, c.p.; (3) *H. sexstrigatus*, Schenck, ♀, c.p.; (4) *H. cylindricus*, F. ♀, c.p.; (5) *Andrena albicans*, K. ♀ ♂, c.p. and s., ab.; (6) *A. albicus*, K. ♂, s.; (7) *A. nana*, K. ♂, s.; (8) *A. argentata*, Smith (= *A. gracilis*, Schenck), ♂, s.; (9) *A. fulvi-*

flattened anthers dehisce edgewise as in *Fragaria*, and only their thin edges remain coated with pollen.

Visitors: A. Hymenoptera—*Apidae*: (1) *Andrena denticulata*, K. ♀ ♂, s. and c.p.; (2) *A. parvula*, K. ♀, c.p. B. Diptera—(a) *Bombyliidae*: (3) *Systæchus sulfureus*, F., s. (Sld.); (b) *Syrphidae*: (4) *Chrysotoxum bicinctum*, L., freq. (Sld.); (5) *Melithreptus scriptus*, L., f.p.; (6) *Cheilosia* sp. (*pictipennis*, Egger?), f.p. See also No. 590, II., and No. 609.

*Potentilla atrosanguinea*, Lodd.—The flowers, according to Delpino, are proterandrous, with short-lived stigmas: in the first stage the anthers are unripe and radiate outwards; in the second, they stand erect on a level with the stigmas. *Andrena* and *Halictus* were observed to visit the flower (178, 360).

*Potentilla argentea*, L.—Twenty species of insect-visitors are enumerated in my *Weitere Beobachtungen*, II.

*Potentilla Salisburgensis*, Haenke (= *P. aurea*, var.  $\beta$ ), *P. aurea*, L., *P. grandiflora*, L., *P. caulescens*, L. (vide *Die Alpenblumen*, pp. 218—222).

*Sibbaldia procumbens*, L.—The honey lies fully exposed, and the tiny, greenish-yellow flowers are abundantly visited by small, short-lipped insects (*Muscidae*, *Ants*, *Ichneumonidae*). Stigmas and anthers ripen simultaneously, but stand too far apart for spontaneous self-fertilisation to take place (609, fig. 87).

#### Tribe Poterieæ.

144. *ALCHEMILLA VULGARIS*, L.—The tiny flowers are destitute of a corolla. A yellow fleshy ring on the inner wall of the



FIG. 76.—*Alchemilla vulgaris*, L.

- 1.—Flower with perfect stamens and short style, from above.
  - 2.—Ditto, viewed obliquely, from above.
  - 3.—Ditto, with three perfect and one abortive stamen, and perfect style.
  - 4.—Ditto, with style still more developed, and all the stamens abortive.
- a, epicalyx; b, calyx; c, stamen; c', abortive stamen; d, stigma; e, nectary.

receptacular tube, which surrounds the style and, later on, the ovary, secretes a thin layer of honey and gives a greenish-yellow appearance, at a little distance, to the whole inflorescence. Owing

to the small supply of honey, insects with long proboscides do not visit the flower or do so sparingly, and beetles and other insects which are only attracted by bright colours are also absent. Cross-fertilisation is favoured by partial separation of the sexes. Flowers seldom occur in which both male and female organs are equally developed. In the great majority of flowers either the stamens are fully developed and the pistil remains so short as scarcely to project above the honey-secreting ring (Fig. 76, 1, 2), or the style is long and exserted (Fig. 76, 4), and the anthers completely aborted: sometimes, however, flowers occur (Fig. 76, 3) in which one or two stamens are developed in addition to the pistil, the others being suppressed.

I have never observed a case of self-fertilisation.

At Lippstadt I have found *Alchemilla vulgaris*, L., visited by one of the Syrphidæ, *Xanthogramma citrofasciata*, Deg.; on the Alps by three butterflies and six flies (*Alpenbl.* pp. 223, 224).

*Alchemilla alpina*, L., *A. fissa*, Günth., and *A. pentaphylla*, L., are frequented by short-lipped insects, and do not differ materially in their arrangements for fertilisation from *A. vulgaris*. They show all transition-stages between hermaphrodite and purely female flowers; and in *A. fissa*, at least, among very many flowers bearing seed I found none with more than one stamen, so that flowers with more than one stamen seem to have lost their female functions (609).

145. AGRIMONIA EUPATORIA, L.—The two styles, which project from the centre of the flower, are united at their base to a fleshy ring, on which I have not observed honey. The five to seven stamens, which are inserted at the edge of this disk, bend slightly inwards; their anthers, which dehisce laterally, stand on a level with the stigmas, and come in contact with them before withering by bending still farther inwards. Insect-visits are scanty, and must, in many cases, induce mainly self-fertilisation, for cross-fertilisation only results when the insects alight well in the centre of the flower. Since all the flowers are found to produce seed, self-fertilisation is doubtless quite efficient.

Eug. Warming gives a thorough description of the development of the flower (762).

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Syritta pipiens*, L.; (2) *Ascia podagrica*, F.; (3) *Melithreptus scriptus*, L.; (4) *M. dispar*, Loew.; (5) *M. pictus*, Mgn.; (6) *M. tæniatus*, Mgn.; (7) *Melanostoma mellina*, L.; (8) *Eristalis tenax*, L., all f.p. only; (9) *Rhingia rostrata*, L., do.; (b) *Muscidæ*:

(10) *Anthomyia* sp., f.p. B. Hymenoptera—*Apidae*: (11) *Halictus*, small species, ♀, c.p.

146. *POTERIUM SANGUISORBA*, L., is anemophilous, with red penicillate stigmas, and anthers hanging out of the flower on long thin filaments. On June 27, 1869, I saw a wasp, *Odynerus parietum*, L. ♀, settle on the flower, attracted probably by the red colour; but after a short and vain search it flew away again.

147. *SANGUISORBA OFFICINALIS*, L.—The flowers are devoid of petals, whose function devolves entirely upon the calyx. The



FIG. 77.—*Sanguisorba officinalis*, L.

- A.—Flower, viewed from above.  
 B.—Ditto, from the side.  
 C.—Ditto, in longitudinal section  
 D.—A sepal, from the inside. ( $\times 7$ .)

calyx, in its lowest<sup>1</sup> part, surrounds the ovary; its middle portion, constituting a fleshy ring around the base of the style, secretes honey; and its uppermost part spreads out into four dark purple sepaline lobes. Anthers (*a*) and stigmas (*st*) are developed simultaneously. The divided stigma resembles that of an anemophilous flower, and is doubtless a character inherited from an anemophilous ancestor resembling *Poterium* (609).

#### Tribe *Rosæ*.

148. *ROSA CANINA*, L.—The upper border of the calyx-tube, internal to the attachment of the stamens, is provided with a thick fleshy ring, which closely surrounds the styles, letting the stigmas only protrude. The flowers seem either to secrete no honey at all,

<sup>1</sup> The lowest and middle part really belong to the receptacular tube.

or only a thin adherent layer of it; at least, I have never found drops of honey, in spite of repeated searching. The flowers, which attract notice by their large petals and their strong scent, compensate the numerous insect-visitors for the want of honey by the abundance of pollen which the numerous stamens supply. The ring surrounding the style is of material importance; for since the stamens, when the flower opens, are inclined outwards and the petals remain directed more or less upwards, the ring and the stigmas within it form the only convenient alighting-place for insects: thus insects coming dusted with pollen from another flower are brought into contact with the stigmas first. And this is the only character present to promote cross-fertilisation, for stigmas and anthers come to maturity together.

In long-continued dull or rainy weather, insect-visits may cease almost completely; but the flowers, turning towards the sun, all stand more or less obliquely, so that part of the pollen falls upon the stigmas.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, c.p.; (3) *Andrena albicans*, K. ♀ ♂, c.p. and f.p.; (3) *A. fucata*, Sm. ♀, c.p.; (4) *Halictus nitidus*, Schenck, ♀, c.p.; (5) *Megachile circumcincta*, K. ♀, c.p.; (6) *Prosopis communis*, Nyl. ♀ ♂, f.p., ab. B. Diptera—*Syrphidae*: (7) *Helophilus floreus*, L.; (8) *Syritta pipiens*, L., ab., both f.p. C. Coleoptera—(a) *Nitidulidae*: (9) *Meligethes*, ab.; (b) *Dermestidae*: (10) *Anthrenus pimpinellæ*, F.; (11) *A. scrophulariæ*, L., both ab., f.p.; (c) *Malacodermata*: (12) *Anthocomus fasciatus*, L.; (d) *Lamellicornia*: (13) *Cetonia aurata*, L.; (14) *Phyllopertha horticola*, L. (both often bite large holes in the petals, and often even devour the stigmas and all the anthers); (e) *Mordellidae*: (15) *Mordella aculeata*, L.; (16) *Anaspis frontalis*, L.; (f) *Cerambycidae*: (17) *Rhagium inquisitor*, F.; (18) *Strangalia armata*, Hbst.; (19) *S. nigra*, L., devouring the anthers and other delicate tissues; (g) *Chrysomelidae*: (20) *Luperus flavipes*.

149. *ROSA CENTIFOLIA*, L.—In consequence of its more conspicuous flowers, this species is still more largely visited by insects; for though I have observed it more rarely than *R. canina*, I have a longer list of its insect-visitors.

A. Hymenoptera—(a) *Apidae*: (1) *Andrena albicans*, K. ♀ ♂, c.p. and f.p., very ab.; (2) *A. pilipes*, F. ♀ ♂, do., scarcer; (3) *A. dorsata*, K. ♀, c.p., ab.; (4) *Halictus zonulus*, Sm. ♀; (5) *H. sexstrigatus*, Schenck, ♀; (6) *H. sexnotatus*, K. ♀, all three c.p.; (7) *Megachile circumcincta*, K. ♀; (8) *M. centuncularis*, L. ♀, both c.p., ab.; (9) *Prosopis propinqua*, Nyl. ♀ ♂; (10) *P. communis*, Nyl. ♀ ♂, both very ab., f.p.; (b) *Chryside*: (12) *Chrysis ignita*, L.; (13) *Chr. cyanea*, L.; (c) *Sphegidae*: (14) *Crabro patellatus*, v. d. L. B. Diptera—*Syrphidae*: (15) *Brachypalpus valgus*, Pz.; (16) *Eristalis æneus*, Scop.; (17) *E. nemorum*, L.; (18) *Chrysogaster viduata*, L.; (19) *Syritta*

pipiens, L., all f.p. C. Coleoptera—(a) *Nitidulidæ*: (20) *Meligethes*, ab.; (b) *Dermestidæ*: (21) *Anthrenus pimpinellæ*, F.; (22) *A. scrophulariæ*, L. ab.; (23) *A. claviger*, Er., scarce; (c) *Malacodermata*: (24) *Dasytes* sp., scarce; (25) *Anthocomus fasciatus*, L., ab.; (d) *Lamellicornia*: (26) *Cetonia aurata*, L.; (27) *Phyllopertha horticola*, L.; (28) *Melolontha vulgaris*, L., all three devouring the soft tissues indiscriminately; (e) *Mordellidæ*: (29) *Mordella aculeata*, L.; (30) *Anaspis ruficollis*, F.; (f) *Cistelidæ*: (31) *Cistela murina*, L.; (g) *Cerambycidæ*: (32) *Strangalia atra*, F.; (33) *S. attenuata*, L.; (34) *Grammoptera ruficornis*, F., very freq.; (35) *Clytus arietis*, L., all feeding on the soft tissues, especially the anthers.

These last two lists not only afford a new example of how increasing conspicuousness leads to more numerous insect-visits; but they also disprove Delpino's theory, that the proper fertilisers of Roses are *Cetoniæ* and *Glaphyridæ* and that therefore the geographical distribution of Roses is limited by the range of these beetles.<sup>1</sup>

*Rosa rubiginosa*, L., produces an obvious secretion of honey (590, II.).

#### Tribe *Pomeæ*.

150. *PYRUS MALUS*, L.—The five stigmas overtop the stamens and ripen before them. The conspicuous flowers and easily accessible honey attract many insects, and cross-fertilisation is insured by the proterogynous condition, and also by the prominent position of the stigmas. In the absence of insects, self-fertilisation results; for most flowers are directed sideways, towards the light, so that pollen can fall of itself upon the stigmas. Here and there flowers occur in which the stigmas are in immediate contact with the anthers.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Bombus terrestris*, L. ♀; (2) *B. agrorum*, F. ♀; (3) *B. lapidarius*, L. ♀; (4) *B. hortorum*, L. ♀, all four very ab.; (5) *Apis mellifica*, L. ♀; (6) *Anthophora pilipes*, F. ♀; (7) *Andrena albicans*, K. ♂ ♀, all seven s. and c.p.; (8) *Halictus sexnotatus*, K. ♀, s.; (9) *Osmia rufa*, L. ♂, s. (the bees almost always alight in the middle of the flowers, and so usually perform cross-fertilisation even in older flowers, since the stigmas are the first to touch the pollen-covered belly of the insect). (b) *Formicidæ*: (10) various species, ab., s. B. Diptera—(a) *Bombyliidæ*: (11) *Bombylius major*, L., s.; (b) *Empidæ*: (12) *Empis livida*, L., s.; (c) *Syrphidæ*: (13) *Rhingia rostrata*, L., very freq., usually s. but also f.p.; (14) *Syrphus pyrastris*, L., s. and f.p.; (d) *Muscidæ*: (15) *Onesia floralis*, R. D., s.; (e) *Bibionidæ*: (16) *Dilophus vulgaris*, Mgn., very ab., s.

<sup>1</sup> *Alcuni App.* p. 18, "Le peonie e le rose debbono arrestarsi dove si arrestano le *Cetoniæ*."

151. *PYRUS COMMUNIS*, L.—The stamens are here longer than the styles, but when the flower opens they are curled inwards and immature, while the stigmas are ripe and project. Cross-fertilisation is insured only if insects come soon after the opening of the flower. In absence of insects, self-fertilisation takes place as in *Pyrus Malus*. I have often observed by experiment how easily pollen from a ripe stamen adheres to the stigmas of a flower, long before its own anthers are ripe.

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Eristalis tenax*, L., very ab.; (2) *E. arbustorum*, L.; (3) *E. nemorum*, L., ab.; (4) *E. intricarius*, L.; (5) *Syritta pipiens*, L.; (6) *Ascia podagrica*, F., both ab.; (7) *Melanostoma mellina*, L., all the *Syrphidæ* both s. and f.p.; (b) *Muscidæ*: (8) *Anthomyia radicum*, R. D. ♂ ♀, very ab.; (9) *Pollenia Vespillo*, F.; (10) *P. rudis*, F.; (11) *Musca corvina*, F.; (12) *M. domestica*, L.; (13) *Lucilia cornicina*, F.; (14) *Calliphora erythrocephala*, Mgn.; (15) *Sepsis* sp., all s.; (16) *Scatophaga merdaria*, F., s. and f.p. B. Hymenoptera—(a) *Apidæ*: (17) *Apis mellifica*, L. ♀, very ab., s. and c.p.; (18) *Bombus terrestris*, L. ♀, s., scarce, and flying away after visiting a few flowers; (19) *Andrena albicans*, K. ♀ ♂, c.p. and s., ab.; (20) *A. Gwynana*, K. ♀; (21) *A. parvula*, K. ♀; (22) *A. Collinsonana*, K. ♀, all both s. and c.p.; (23) *Halictus rubicundus*, Chr. ♀, c.p. and s.; (b) *Formicidæ*: (24) *Lasius niger*, L. ♀, l.h.; (c) [*Tenthredinidæ*: (25) *Dolerus gonager*, Kl., scarce; (26) *Nematus caprææ*, L., freq., s. C. Coleoptera—(a) *Nitidulidæ*: (27) *Meligethes*, ab.; (b) *Curculionidæ*: (28) *Rhynchites æquatus*, L.; (c) *Coccinellidæ*: (29) *Coccinella 14-punctata*, L.; (d) *Phalacridæ*: (30) *Olibrus æneus*, F., all four licking honey. D. Thysanoptera—(31) *Thrips*, ab.

152. *PYRUS AUCUPARIA*, Gært.—When the flower opens, the stamens are still immature, the outer ones standing erect, the inner ones bent inwards so that their anthers are placed below the stigmas. The stigmas are ripe, and project in the centre of the flower. The anthers, which open inwards, cover themselves all round with pollen. In cold, dull weather, the innermost anthers remain bent down below the stigmas even after dehiscence; the outer ones stand above the stigmas, incurved towards them; thus, in absence of insects, self-fertilisation takes place readily. On the other hand, in warm sunshine, the stamens are inclined away from the stigmas, and the honey-secreting ring is visible between, protected with hairs issuing from the base of the style. Insects, in dipping down to the honey, touch stamens and stigmas with opposite sides of their heads. The small flowers are rendered conspicuous by aggregation, and the rich supply of honey attracts very numerous insects.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, s. and c.p., very ab.; (2) *Andrena albicans*, K. ♀ ♂; (3) *A. albicans*, K. ♀, very

ab. ; (4) *A. dorsata*, K. ♀ ♂, all three sucking and collecting pollen ; (5) *A. Smithella*, K. ♀, c.p. ; (6) *A. atriceps*, K. ♀ ; (7) *A. convexiuscula*, K. ♀ ; (8) *Halictus rubicundus*, Chr. ♀ ; (9) *H. zonulus*, Sm. ♀, all sucking and collecting pollen ; (10) *Nomada ruficornis*, L. ♀ ♂ ; (11) *N. signata*, Jur. ♀, both sucking ; (b) *Formicidæ* : (12) *Formica congerens*, N. ♀ ; (13) *Lasius niger*, L. ♀ ; (14) *Myrmica* sp., ♀, all three s., ab. B. Diptera—(a) *Empidæ* : (15) *Empis livida*, L. ; (16) *E. rustica*, Fallen, both s., ab. ; (b) *Syrphidæ* : (17) *Helophilus florens*, L. ; (18) *Eristalis arbustorum*, L. ; (19) *E. nemorum*, L. ; (20) *E. horticola*, Mgn. ; (21) *Rhingia rostrata*, L., all five s. and f.p., ab. ; (c) *Muscidæ* : (22) *Echinomyia fera*, L. ; (23) *Onesia floralis*, R. D. ; (24) *Scatophaga stercoraria*, L. ; (25) *S. merdaria*, F., the last three ab., s. ; (26) *Sepsis*, ab. ; (d) *Conopidæ* : (27) *Myopa testacea*, L. ; (e) *Bibionidæ* : (28) *Dilophus vulgaris*, F., ab., s.,—besides several undetermined flies and midges. C. Coleoptera—(a) *Nitidulidæ* : (29) *Epurea* ; (30) *Meligethes*, both in hundreds ; (b) *Dermestidæ* : (31) *Byturus*, in hundreds ; (32) *Attagenus pello*, scarce ; (c) *Elateridæ* : (33) *Agriotes aterrimus*, L. ; (34) *Dolopius marginatus*, L. ; (35) *Corymbites holosericeus*, L. ; (36) *Limonium cylindricus*, Pk. ; (37) *L. parvulus*, Pz. ; (d) *Lamellicornia* : (38) *Cetonia aurata*, L. ; (39) *Melolontha vulgaris*, L., both devouring all the tissues of the flower ; (e) *Malacodermata* : (40) *Malachius æneus*, F., l.h., and devouring the anthers ; (f) *Mordellidæ* : (41) *Anaspis rufilabris*, Gylh. ; (g) *Tenebrionidæ* : (42) *Microzom tibiale*, F. !—only once ; (h) *Curculionidæ* : (43) *Apion* sp. ; (44) *Phyllobius maculicornis*, Germ., both s. ; (i) *Cerambycidæ* : (45) *Clytus arietis*, L., s. ; (k) *Chrysomelidæ* : (46) *Adimonia sanguinea*, F., s.

153. *CRATÆGUS OXYACANTHA*, L.—The flowers resemble those of *Pyrus Aucuparia* in regard to their proterogyny, the manner of dehiscence and the bending inwards of their stamens, and hence also in the great likelihood of cross-fertilisation. The outer stamens begin to dehisce one or two days after the opening of the flower. Dung-flies and flesh-flies are attracted in special abundance by the odour of the flowers. In absence of insects, many flowers fertilise themselves. The young shoots sometimes exude a sweet sap, which is sought by insects. On May 9, 1868, on bushes that were just beginning to flower, I saw *Anthophora pilipes*, F. ♂, *Bombus terrestris*, L. ♀, an *Andrena*, and *Odynerus parietum*, L. ♀, all feeding on this sap.

Visitors : A. Diptera—(a) *Empidæ* : (1) *Tachydromia connexa*, Mgn., ab. ; (2) *Empis livida*, L., s., very ab. ; (3) *Microphorus velutinus*, Macq. (identified by Herr Winnertz) ; (b) *Syrphidæ* : (4) *Pipiza notata*, Mgn. ; (5) *Rhingia rostrata*, L., s., very ab. ; (6) *Eristalis tenax*, L. ; (7) *E. intricarius*, L. ; (8) *E. nemorum*, L. ; (9) *E. arbustorum*, L. ; (10) *E. sepulcralis*, L. ; (11) *E. pertinax*, Scop.,—all the species of *Eristalis* s. and f.p. ; all except *E. intricarius* very ab. ; (12) *Helophilus florens*, L. ; (13) *H. pendulus*, L., both ab. (14) *Xylota segnis*, L. ; (c) *Muscidæ* : (15) *Echinomyia fera*, L. ; (16) *Sarcophaga carnaria*, L., s. ; (17) *Onesia floralis*, R. D., s. ; (18) *O. sepulcralis*, Mgn., s. ; (19) *Graphomyia*

maculata, Scop. ; (20) *Mesembrina meridiana*, L. ; (21) *Cyrtoneura* sp. ; (22) *Aricia serva*, Mgn. ; (d) *Bibionidæ* : (23) *Bibio Marci*, L., s. ; (24) *Dilophus vulgaris*, L., very ab. B. Coleoptera—(a) *Dermestidæ* : (25) *Attagenus pello*, L., l.h. ; (26) *Anthrenus scrophulariæ*, L., very ab. ; (27) *A. pimpinellæ*, F., still more ab. ; (28) *A. claviger*, Er., scarce, all three l.h. ; (b) *Nitidulidæ* : (29) *Meligethes*, l.h., very ab. ; (c) *Buprestidæ* : (30) *Anthaxia nitidula*, L. ; (d) *Malacodermata* : (31) *Malachius (elegans, Ol. ?)*, feeding on the anthers ; (32) *Telephorus testaceus*, L. ; (e) *Ædemeridæ* : (33) *Asclera cœrulea*, L. ; (f) *Mordellidæ* : (34) *Anaspis frontalis*, L., l.h. ; (35) *Mordella abdominalis*, F., l.h. ; (g) *Cerambycidæ* : (36) *Clytus mysticus*, L., l.h. ; (37) *Grammoptera ruficornis*, F., ab., l.h. ; (h) *Chrysomelidæ* : (38) *Clythra cyanea*, F., gnawing the petals. C. Hymenoptera—*Apidæ* : (39) *Andrena Schrankella*, Nyl. ♂, s. ; (40) *A. helvola*, L. ♀, s. ; (41) *A. fulvicrus*, K. ♀ ♂, s. ; (42) *A. nitida*, K. ♀ ♂, very freq., s. and c.p. ; (43) *A. varians*, Rossi, ♀ ; (44) *A. Trimmerana*, K. ♀ ♂ ; (45) *A. atriceps*, K. ♀ ♂ ; (46) *A. Gwynana*, K. ♀ ; (47) *A. fulva*, K. ♀ ; (48) *A. albicans*, K. ♀ ♂, very ab. ; (49) *A. dorsata*, K. ♀ ; (50) *A. chryso-sceles*, K. ♀ ; (51) *A. parvula*, F. ♀ ; (52) *A. connectens*, K. ♀, the last ten both s. and c.p. ; (53) *Halictus cylindricus*, K. ♀, s. ; (54) *Nomada ruficornis*, L. ♀ ♂, s. ; (55) *N. signata*, Jur. ♀ ; (56) *Eucera longicornis*, L. ♂, s. ; (57) *Apis mellifica*, L. ♀, s. and c.p., ab.

154. *COTONEASTER VULGARIS*, Lindl.—This plant in the Alps often grows on the same rocks to which a wasp (*Polistes gallica*)



FIG. 78.—*Cotoneaster vulgaris*, Lindl.

A.—Flower, in slightly oblique side view.

B.—Ditto, from above.

C.—Ditto, in longitudinal section.

n, nectary. (× 7.)

(From Rosegthal, Pontresina, June 18, 1879.)

has attached its stalked, open nest. The hemispherical calyx of the flower is filled with honey, which the petals arch over and protect, excluding a great many insects. I have found the flowers visited solely by the above-mentioned wasp, whose head just fits into the flower. Cross-fertilisation is insured by proterogyny; in absence of insects, self-fertilisation occurs (609).

*Amelanchier vulgaris*, Moench. (*Aronia rotundifolia*, Pers.).—This plant is imperfectly proterandrous. Of the three whorls of stamens, the outermost dehisce, while the others are still bent inwards and shelter the immature stigmas. The inner anthers and the stigmas are ripe together (609).

#### REVIEW OF THE ROSACEÆ.

In all honey-yielding Rosaceæ the honey is secreted and carried by an annular region (*disk*) of the inner wall of the receptacular tube, sometimes closely surrounding the pistil, sometimes shifted farther outwards: this ridge shows all transitions between abundant and evident drops of honey, a thin sweet layer invisible to us but eagerly licked by insects, and, lastly, absolute barrenness.

The abundance of insect-visits depends here, as elsewhere, on the conspicuousness of the flowers and the amount of spoil they furnish; and, similarly, the variety of insects which frequent the flowers depends on the accessibility of the spoil. For instance, the small, yellow, honeyless flowers of *Agrimonia Eupatoria* are sparingly visited by a few pollen-feeding *Syrphidæ* and pollen-collecting bees; while the equally honeyless roses attract a very numerous company of insects, which come for the sake of the pollen and the delicate tissues of the flower. The effects of conspicuousness are well illustrated by the Raspberry and the Blackberry. The effect of diminished accessibility of the honey in restricting the variety of insect-visitors is shown in the case of *Geum rivale*; the flowers of which remain half-closed, and, though yielding abundant honey, are only visited by specially long-tongued bees and flies (*Bombus* and *Rhingia*): the Raspberry and Blackberry may be contrasted to illustrate this point also.

In Rosaceæ whose honey lies concealed and which are fertilised by a motley crowd of short-lipped insects, the flowers are for the most part greenish-yellow, yellow, or white in colour; in *Comarum palustre*, *Potentilla atrosanguinea*, and *Sanguisorba officinalis* they are dark-red or purple, probably owing to the influence of carrion-feeding flies.

In Rosaceæ whose honey lies more deeply placed, which are mainly fertilised by long-tongued bees, we find in part red colours

(*Amygdalus Persica*, *Cydonia japonica*). In this relation the genus *Geum* is interesting; for that species which is fertilised by bees (*G. rivale*) exhibits a red colour in which the influence of the primitive yellow is still evident.

Rosaceæ visited for the sake of their pollen have white flowers when their chief visitors are small, short-lipped insects (*Spiræa Ulmaria*, *S. Aruncus*); but show a tendency to red when frequented mainly by bees or *Syrphidæ* (*Rosa*). In the whole order of Rosaceæ no species seems to have acquired a violet or blue flower, nor to have become adapted exclusively for fertilisation by Lepidoptera.

#### ORD. SAXIFRAGACEÆ.

##### Tribe *Saxifrageæ*.

Dr. A. Engler<sup>1</sup> has investigated thirty-eight species of *Saxifraga* and found them to be all proterandrous with movement of the stamens singly in succession towards the middle of the flower. On the other hand, he found *Bergenia* (*Saxifraga crassifolia*, L.), *Mitella*, L., *Heuchera*, L., and *Drummondia*, DC. (= *Mitella pentandra*, Hook.) to be proterogynous without movement of the stamens (221). On species of *Saxifraga* flowering in the open air he observed beetles (*Haltica*, small *Staphylineæ*), flies, and especially bees. He doubts Sprengel's interpretation of the so-called honey-guides (Saftmal), for though present in some Saxifrages they are absent in others. In plants whose honey varies between fully exposed and hidden situations, such a fluctuation of the guiding marks is very natural, and rather strengthens Sprengel's theory.

In my *Alpenblumen* I have tried to prove that those species of *Saxifraga* which have dotted petals show all transitions from mere adornment by which insects are attracted to ornamentation which serves also as a "pathfinder."

The proterandrous flowers of *S. aizoides*, L., and *S. oppositifolia*, L., are figured by Axell (17).

*Saxifraga sarmientosa*, L. fil., has asymmetrical flowers (Todd, 722).

Of the numerous Alpine species of *Saxifraga*, I have examined and figured thirteen. All show, more or less distinctly, the peculiarity that the anthers ripen one after another; at the same

<sup>1</sup> "Monographie der Gattung *Saxifraga*," p. 26. Breslau, 1872.

time they bend in towards the centre of the flower, but after dehiscing they again move outwards. This peculiarity was known to Treviranus, but was explained by him as aiding self-fertilisation (742). On the contrary it aids cross-fertilisation, by causing the insect-visitors to come in contact with the pollen-dusted anthers.

In most of the species of *Saxifraga* which I have investigated (*S. rotundifolia*, L., *S. stellaris*, L., *S. aspera*, DC., *S. bryoides*, L. = *S. aspera*, var.  $\beta$ , *S. aizoides*, L., *S. Aizoön*, Jacq., *S. cæsia*, L.,

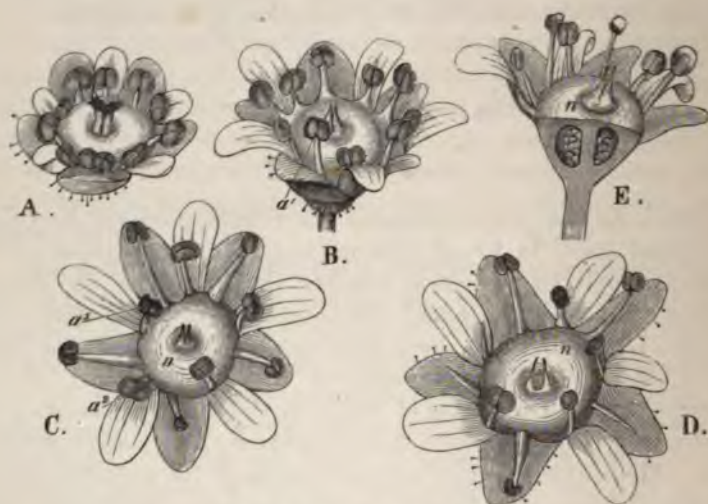


FIG. 79.—*Saxifraga Seguieri*, Spreng.

A.—Flower, in first (female) stage, seen obliquely from above. The stigmas are mature. Anthers, petals, and sepals are still far from their full size.

B.—Flower, at commencement of second (male) stage. The stigmas are shrivelled at the tip, the anthers are all still closed. ( $a'$  dehiscence while the drawing was being made.)

C.—Flower, at the beginning of the second half of the second (male) stage. The five outer anthers are already empty; of the five inner,  $a'$  has dehiscence, and  $a''$  is in the act of dehiscing. The stigmas are entirely shrivelled up.

D.—A still older flower. Of the five inner anthers three are still covered with pollen, one is still closed.

E.—Section of flower in second stage. ( $\times 7$ .)

*S. exarata*, Vill., *S. stenopetala*, Gaud.), the stigma only ripens after the anthers have withered. Engler thought that this was the case in all the species, but *S. oppositifolia*, L., and also *S. tridactylites*, L., a lowland species, are only feebly proterandrous in certain localities, and in others are feebly proterogynous; and three species, *S. androsacea*, L., *S. muscoides*, Wulf., and *S. Seguieri*, Spr., I have found to be everywhere distinctly proterogynous, only the first of the three being able in case of need to fertilise itself.

As in dioecious entomophilous plants the male flowers are

usually larger and more conspicuous than the female, so in the three distinctly proterogynous species of *Saxifraga*, the flowers while in their male stage are more than twice as large as they were at first while in their female stage. As Sprengel supposed, it is probable that many insects are thus induced to visit the male flowers first, and then, having dusted themselves with pollen, to proceed to the female flowers and fertilise them. The annexed figure may serve to show this distinction between the flowers in their male and female stages.

The honey is quite visible in the above-named species of *Saxifraga*, except *S. oppositifolia*. Very various short-lipped insects, but especially flies, serve therefore as fertilising agents. To the selective influence of flies, therefore, the development of the ordinary colours—white, dull-yellow, white with yellow or purple spots—must be mainly ascribed. In particular, the prettily dotted petals of *S. rotundifolia* and *S. umbrosa*, L., seem to be due to the influence of certain elegant and prettily coloured *Syrphidæ* by which they are especially visited and cross-fertilised (*S. rotundifolia* by *Spehegina clunipes* and *Peleccera scævoides*; *S. umbrosa* by *Ascia podagrica*).

*Saxifraga aizoides*, L., with its large golden flowers dotted with orange, is the most conspicuous form, and attracts most insect-visitors. I have found it to be visited by 126 species of insects (Coleoptera, 8; Diptera, 85; Hymenoptera, 20; Lepidoptera, 13). (609.)

The honey is most deeply placed in *S. oppositifolia*; the flowers of this species are diligently and persistently visited by butterflies and are arrayed in carmine or purple, the favourite colour of most of these insects.<sup>1</sup>

155. *CHRYOSPLENIUM ALTERNIFOLIUM*, L.—The flowers have a great superficial likeness to the apical flowers of *Adoxa*, and are visited by a very similar set of tiny insects.

From the middle of the flower the two styles stretch, diverging and bending outwards slightly, capped at the apex by the smooth, capitate stigmas, and surrounded at the base by a broad, fleshy, yellowish disk, secreting numerous minute drops of honey. At the edge of this disk the calyx, which coalesces below with the ovary, expands horizontally into four broad rounded sepals, bright yellow, and slightly recurved. There is no trace of petals. Between each pair of sepals, and also facing each one, there stands on the edge of the disk a stamen, erect, and reaching as high as the

<sup>1</sup> 609, Figs. 26-38; in connection with *S. umbrosa*, see 604.

styles. First the four outer ones, which stand opposite the sepals, ripen one after the other, and then the other four. All the stamens dehisce on both sides, and flap open so widely that they are covered almost all round and also above with pollen. The stigmas are susceptible of fertilisation during the whole time of flowering. A number of such flowers, from five to upwards of a dozen, are closely packed in an almost level cyme, and, together with the broad green bracts that lie nearly in the same plane, form a conspicuous expanse with a golden-yellow centre.

Numerous minute insects of different orders are attracted. Most of them touch a stigma with one part of their body, and with another one or more of the anthers; and so cross-fertilisation is promoted. But self-fertilisation is not unfrequently induced by the tiny guests that creep irregularly about the flower. In default of insect-visits, self-fertilisation can only take place in a perpendicular or nearly perpendicular position of the flowers; for only then can pollen fall upon the stigmas. On April 13, 1872, I collected forty-six insects upon flowers growing in the shade.

A. Diptera—(a) *Muscidae*: (1) Five specimens of *Sciomyza cinerella*, Fallen; (b) *Simulidae*: (2) *Simulia* sp., three specimens; (c) *Cecidomyiidae*: (3) Six specimens; (d). *Mycetophilidae*: (4) Five specimens; (e) *Chironomidae*: (5) Three specimens, besides minute species. B. Hymenoptera—(a) *Formicidae*: (6) *Lasius niger*, L. ♀, eight specimens; (7) *Myrmica ruginodis*, N. ♀ (+), two specimens; (8) *M. lævinodis*, N. ♀, three specimens; (b) *Cynipidae*: (9) *Eucoila*, Westw. (*Cothonaspis*, Hart.), one specimen. C. Coleoptera—(a) *Phalacridae*: (10) *Olibrus æneus*, F. one specimen; (b) *Lathridii*: (11) *Corticaria gibbosa*, Hbst., two specimens; (c) *Curculionidae*: (12) *Apion varipes*, Germ., four specimens; (13) *A. onopordi*, K., three specimens; all the visitors were licking honey.

Also, I found small snails (young *Succineæ*) upon many flowers, either creeping about, or devouring the stigmas or anthers. In the slimy matter left upon the flowers, pollen-grains could as a rule be recognised: in several cases I could distinctly see that pollen was placed upon a stigma by help of the snails.

Now if, under some changed conditions, insect-visits altogether failed, it would obviously be of advantage to the plant to have cross-fertilisation promoted by the snails, at least on the supposition that by new modifications the ravages of the snails should be obviated. This example may explain the origin of such a floral arrangement as Delpino observed in *Alocasia odora* and *Rhodea japonica*. And so the doubt which I formerly published concerning the truth of Delpino's theory is now removed.

*Chrysosplenium oppositifolium*, L., is protogynous with persistent stigmas (78).

156. *BERGENIA* (*SAXIFRAGA*) *CRASSIFOLIA*, L.—I saw (April 4, 1868) hive-bees and *Bombus hortorum*, L. ♀, greedily sucking honey on this plant, and found pollen on the stigmas of several flowers whose anthers were not yet open.

157. *PARNASSIA PALUSTRIS*, L.—Sprengel described very fully the structure of this plant, but remained in doubt not only as to

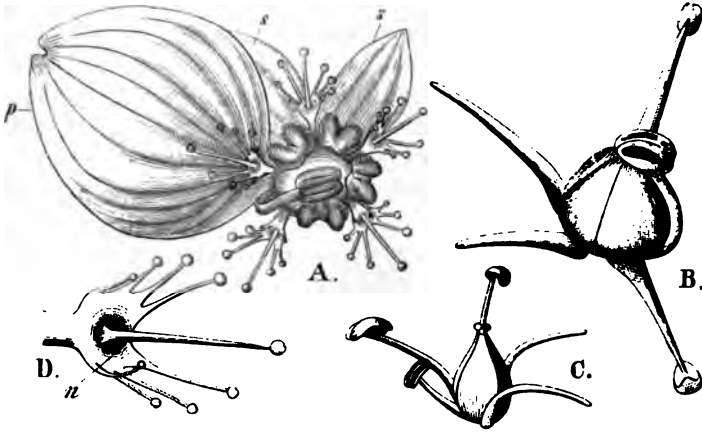


FIG. 80.—*Parnassia palustris*, L.

A.—Flower, seen from above, after removal of three sepals and four petals. The flower had just opened. One stamen has risen up and placed its anther on the centre of the pistil, whose stigmas are not yet mature; the anther is on the point of dehiscing, and will cover its upper surface with pollen.

B.—Essential organs of a flower, in which four stamens have shed their pollen; the fifth lies, covered with pollen, upon the pistil. The stigmas are not yet developed.

C.—Essential organs of a flower in the second (female) condition. (A—C,  $\times 5\frac{1}{2}$ .)

D.—A staminode, more magnified.

its fertilisers, but even whether it was diurnal or nocturnal. Hildebrand has observed *Helophilus florens*, L., upon its flowers.

The anthers before maturity lie close upon the conical ovary, which rises up in the middle of the flower and overtops them; they ripen slowly one after the other, each in turn elongating till it brings its anther immediately over the end of the pistil, and then dehiscing on the upper surface. It afterwards bends outwards and is succeeded by another, and finally, when all the anthers have dehised and moved away, the stigma becomes developed.

The curious nectaries stand immediately opposite to the petals, alternating with the stamens. Each consists of a short, broad peduncle, broadening above into a fleshy disk, which secretes

honey in two shallow depressions on its inner side, leaving it fully exposed. Above it gives off seven to eighteen yellow, knobbed, glandular bodies, which surround the upper portion of the ovary and are probably of service in making the nectaries more obvious to flies which alight in the middle of the flower.

These yellow knobs placed at the ends of the hairs look so exceedingly like drops of fluid that it needs special examination to convince one that they are perfectly dry. An observation of my son Hermann's proves that even flies are deceived by this appearance; he observed from a very short distance a specimen of *Eristalis nemorum* trying to lick these bodies for a long time, until at last it flew away on his coming closer.

We have thus in *Parnassia palustris* a very well-marked example of a *deceptive flower*, which deludes the foolish flies by displaying a multitude of conspicuous but sham drops of honey; and which, after thus alluring them, affords them indeed some easily accessible honey, which repays their trouble but is quite incommensurate with the apparently bountiful display. The smaller flies generally travel round the flower, to reach all the nectaries; the larger ones rest in the middle of the flower for this purpose, and so dust their under sides with pollen in younger flowers and accomplish cross-fertilisation on passing to older ones.

Visitors: A. Diptera—(a) *Syrphidae*: (1) *Eristalis nemorum*, L., s. ab.; (2) *E. arbustorum*, L., s. ab.; (3) *Helophilus florens*, L., s. ab.; (4) *Syrphus ribesii*, L., s. ab.; (5) *S. balteatus*, Deg., very ab., s.; sometimes f.p.; (6) *S. pyrastris*, L., ab. s.; (7) *S. excisus*, Zett., s.; (8) *Melanostoma mellina*, L., s.; (9) *Melithreptus scriptus*, L., s.; (10) *M. menthastri*, L., s.; (11) *M. tæniatus*, Mgn., s.; (12) *Syrpitta pipiens*, L., ab. s.; (b) *Muscidae*: (13) *Sarcophaga carnaria*, L., s.; (14) *Pollenia vespillo*, F., s.; (c) *Tipulidae*: (15) *Tipula oleracea*, L. B. Hymenoptera—(a) *Tenthredinidae*: (16) *Tenthredo* sp., s.; (b) *Ichneumonidae*: (17) Many small species, s.; (c) *Sphegidae*: (18) *Pompilus viaticus*, L.; (19) *Gorytes campestris*, L. C. Coleoptera—(20) *Coccinella 7-punctata*, L.; (21) C. 14-punctata, L., both very ab., l.h. A list of Alpine visitors (including 43 Diptera) is given in No. 609.

#### Tribe *Hydrangeæ*.

*Philadelphus coronarius*, L., is proterogynous. When the flower opens the stigmas are already ripe, but the stamens still immature. In weather favourable for insect-visits, it is easy to find flowers whose anthers are still closed but whose stigmas are sprinkled with pollen. The numerous anthers stand, both before and after dehiscence, close round the stigma, some on a level with it, some higher, some lower; the outermost dehisce first, the innermost last; all cover themselves all round with pollen. Honey is secreted

by a white, fleshy disk on the upper surface of the ovary. Insect-visitors, collecting or feeding on pollen or thrusting their heads down between the stamens towards the honey, can thus lead to cross-fertilisation only in young flowers, but in old ones cross-fertilisation and self-fertilisation are alike possible. In absence of insects, self-fertilisation may easily take place, for the stigmas stand partly in the line of fall of the pollen. But the honey, only hidden by the stamens, is accessible to so many insects, and the white colour and strong scent are such powerful attractions, that in fine weather insect-visits can seldom fail.

Tribe *Ribesicæ*.

158. *RIBES ALPINUM*, L.—This species presents its honey in a shallower depression than any of our other species of *Ribes*, so

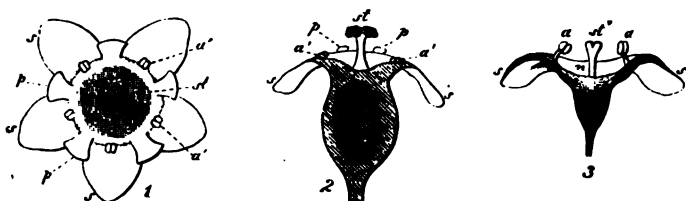


FIG. 81.—*Ribes alpinum*, L.

- 1.—Female flower, from above.  
2.—Ditto, in section.  
3.—Male flower, in section.  
a, rudimentary anthers; st, rudimentary stigma; n, nectary.

that it is easily accessible to very various insects, and is consequently visited by the most manifold forms. Although I only had an opportunity of watching a few plants in a hedge, I saw upon their flowers the following :

A. Hymenoptera—*Apidae* : (1) *Andrena albicans*, K. ♀ ♂, s. and f.p., very ab. ; (2) *A. Gwynana*, K. ♂, s. ; (3) *A. nana*, K. ♂, s. ; (4) *Halictus nitidus*, Schenck, ♀, s. ; (5) *H. nitidiusculus*, K. ♀, c.p. ; (6) *Sphecodes gibbus*, L. ♀, s. B. Diptera—(a) *Muscidae* : (7) *Scatophaga stercoraria*, L. ; (8) *S. merdaria*, F. ; (b) *Syrphidae* : (9) *Syritta pipiens*, L., all three ab., s.

Upon this abundance of insect-visits, which insures cross-fertilisation, depends the dioecism, evolved from a previous hermaphroditism and still showing traces thereof, which would of necessity be fatal in default of insect-visits. The male flowers are of scarcely larger size, but their greenish-yellow colour is more conspicuous than the green female flowers. The calyx almost alone plays the part of signal to the insects.

159. *RIBES NIGRUM*, L.—The stigma and anthers are both alike ripe at the opening of the flowers. The anthers open on the inner side, and are brought so close to the stigma by the convergence of the petals that an insect's head, when pushed into the flower, must touch with one side the pollen-dusted face of one or



FIG. 82.—*Ribes nigrum*,  
L.  
Lateral view of flower.

two anthers, and with the other, at the same time or a little before, the slightly protruding stigma. Since the bell-shaped calyx, whose floor secretes honey, is 5 mm. deep, and the red tips of the sepals and the small white petals make the pendulous flowers only slightly conspicuous, insect-visits are not plentiful: I have only seen the honey-bee sucking at this species. It put its head only once into each flower, and touched the stigma now on the upper side, now on the lower, sweeping

away pollen each time on the opposite side and so regularly accomplishing cross-fertilisation. As compensation for the paucity of insect-visits, self-fertilisation takes place regularly in unvisited flowers, pollen falling of itself out of the anthers upon the recurved margin of the stigma.

160. *RIBES RUBRUM*, L., is likewise homogamic, but has much flatter, more widely open, and more conspicuous flowers than *R. nigrum*, and more easily accessible honey. So it is more abundantly visited by insects, and is cross-fertilised after the same manner as *R. nigrum* but is self-fertilised less easily; the flowers are turned sideways, and self-fertilisation only takes place when pollen falls upon the stigma from the anthers above it. I have seen the following insects upon the flowers:—

Hymenoptera—(a) *Apidae*: *Andrena fulva*, Schrank, ♀, s. and c.p., freq.; (2) *A. Smithella*, K. ♂, s.; (3) *A. nana*, K. ♂, s.; (4) *Apis mellifica*, L., ♀, s. and c.p., ab.; (b) *Tenthredinidae*: (5) *Nematus hortensis*, Htg., s.

161. *RIBES GROSSULARIA*, L.—The anthers dehisce when the flower opens: the styles have not as yet attained their full length, nor have the stigmas developed their papillæ. Since the flowers mostly hang down perpendicularly and the stamens stand around, and on a level with, the stigmas, self-fertilisation can as a rule not take place, even in default of insect-visits. This, like the proterandry, points to more numerous insect-visits than the former species receives; and these really take place, induced by the large recurved sepals, the large, perpendicular, downward-pointing petals, and the easily accessible honey.

Visitors : A. Hymenoptera—*Apidæ* : (1) *Bombus terrestris*, L. ♀, freq. ; (2) *B. pratorum*, L. ♀ (in Stromberg), very ab. ; (3) *B. Scrimshiranus*, K. ♀ ; (4) *Apis mellifica*, L. ♀, very ab. ; (5) *Andrena nitida*, K. ♂, all sucking ; (6) *A. albicans*, K. ♂ ♀ ; (7) *A. Gwynana*, K. ♂ ♀ ; (8) *A. fulva*, Schrank, ♀, the last three both s. and f.p. ; (9) *Halictus rubicundus*, Chr. ♀, s. B. Diptera—(a) *Muscidæ* : (10) *Scatophaga stercoraria*, L., s. ; (11) *Calliphora erythrocephala*, Mgn., s. ; (b) *Syrphidæ* : (12) *Eristalis æneus*, L., s. and f.p. ; (13) *Syritta pipiens*, L., do. The insect-visitors cause cross-fertilisation in the same way as in *R. nigrum*. See also No. 590, 1.

*Ribes sanguineum*, Pursh.—The calyx-tube is 3 mm. deep ; the erect petals form a tube more than 5 mm. deep. As a rule, therefore, the honey is obtained and the flowers fertilised by bees only, especially the hive-bee.

*Ribes aureum*, Pursh.—The calyx-tube is 10 to 11 mm. deep, and the erect petals add 3 mm. more to its depth. The honey is only accessible to very long-tongued bees, and the flowers have been found by Delpino in Italy and by me in Lippstadt to be visited only by *Anthophora pilipes*, ♀, whose proboscis is the longest among our native bees (20 mm.). In the two last species the flowers persist a long time after the reproductive organs are withered, and even become more conspicuous, since the petals in *R. sanguineum* change from white to pink, and those of *R. aureum* from bright yellow to carmine. By this peculiarity, not only is the power of attracting insects increased, but the more intelligent fertilising agents are told at the first glance which flowers contain no more treasure for them, the result being that they visit and fertilise more flowers in the same time (590, 1.). The same kind of colour-change occurs in several species of *Fuchsia* and *Lantana*, in *Diervilla* (*Weigelia*) *rosea*, *Melampyrum pratense*, L., *Fumaria capreolata*, var. *pallidiflora*, Jord., and others (575).

*Ribes petraeum*, Wulf., is, according to Ricca, slightly protogynous (665) ; according to my own observations it is homogamic (609).

#### ORD. CRASSULACEÆ.

*Bryophyllum calycinum*, Salisb., is proterandrous, and has hanging, tubular flowers, rich in honey. Delpino supposes humming-birds to be the fertilisers, despite the pale greenish colour (177).

162. *SEDUM ACRE*, L.—Although the plant is small, it is rendered conspicuous on the bare spots where it grows by its

the closely packed flowers, to suck honey or gather pollen, come at once in contact with the stamens or stigmas of many flowers, and, as a rule accomplish cross-fertilisation by help of the proterandrous condition: old flowers alone, which retain some pollen upon their stamens when the stigmas are ripe, are liable to self-fertilisation.

In spite of the smaller flowers and more hidden honey, this species can dispense with the possibility of self-fertilisation, since the close association of many flowers insures insect-visits and consequent distribution of pollen more completely than is the case in *Sedum acre*. Although I only once watched the flowers of *Sedum Telephium* (August 16, 1869) in sunny weather I saw the following insects visit it:—

A. Hymenoptera—(a) *Apidae*: (1) *Bombus* (*Apathus*) *campestris*, Pz. ♂; (2) *B. silvarum*, L. ♀ ♂, freq.; (3) *B. agrorum*, F. ♂, these three sucking; (4) *B. lapidarius*, L. ♀, c.p.; (5) *Halictus zonulus*, Sm. ♀, s.; (b) *Tenthredinidae*: (6) *Allantus notha*, Kl. (Tekl. B.). B. Diptera—*Muscidae*: (7) *Echinomyia magnicornis*, Zett., s.

*Sedum atratum*, L., is, according to Ricca, proterogynous with short-lived stigmas (665). I have found it, however, on the Alps to be likewise proterogynous, but liable to regular and even early spontaneous self-fertilisation, which is probably indispensable, as the plant is but little visited by insects (609).

*Sedum repens*, Schleich.—This species also is proterogynous on the Alps, and in the absence of insects it likewise fertilises itself; but its flowers are rather conspicuous and more visited by insects, so that the need for self-fertilisation is less urgent than in the case of *S. atratum* (609).

#### THE COLOUR AND SIZE OF THE FLOWER IN CRASSULACEÆ.

The colour of the flower in Crassulaceæ depends closely upon the adaptation of the flower to a narrow or wide circle of visitors. In the species of *Sedum*, whose honey is still quite visible and accessible to the most short-lipped insects, the flowers are greenish-yellow, yellow, or white; in *Sempervivum Funkii*, Braun., *S. montanum*, L., *S. arachnoideum*, L., and *S. tectorum*, L., whose honey lies hidden, and which I have seen visited on the Alps by a miscellaneous company of bees, Lepidoptera, and long-tongued flies, the flowers are purple; in *Sempervivum Wulfenii*, Hopp., whose honey is still more concealed, the flowers, which are chiefly visited

by humble-bees, are sulphur-yellow, and only remain purple at the base. I say *only remain* purple at the base, because this colouring is now useless, and seems only explicable as a remnant inherited from purple-flowered ancestors. The sulphur-yellow colour of *Sempervivum Wulfenii* seems not to stand on the same rank as the yellow colour of some Sedums; but rather to have been developed from a purple colour by the selective influence of humble-bees. In connection with the size of the flower, we see in many Crassulaceæ the number of the parts increased or decreased: increased in *Sedum* from 5 to 7, in *Sempervivum arachnoideum* to 9—11, in *S. montanum* to 9—12, in *S. Funkii* to 10—13, in *S. tectorum* to 11—13, in *S. Wulfenii* to 13—16; decreased in *Bulliarda*, DC., to 4, in *Tillæa*, L., to 3 (609).

#### ORD. DROSERACEÆ.

*Drosera*, L., occurs with cleistogamic flowers (169).

#### ORD. HALORAGACEÆ.

*Callitriche verna*, L.—The proterogynous flowers are figured by Axell (17). Axell considers them to be anemophilous; Ludwig looks upon the submerged flowers as hydrophilous, and the others as entomophilous (435).

*Myriophyllum spicatum* is anemophilous, and *M. verticillatum* is partly anemophilous and partly hydrophilous, according to Ludwig (435).

#### ORD. COMBRETACEÆ.

*Combretum*, L., is very diligently visited by humming-birds in South Brazil (Fritz Müller, 359). My brother informs me by letter that it is also frequented by butterflies (*Callidryas*).

#### ORD. MELASTOMACEÆ.

*Heeria*, Schlecht., has two kinds of stamens, one serving, apparently, to attract the fertilising-agents, and the other supplying the pollen for cross-fertilisation (606).

#### ORD. LYTHRARIÆ.

165. *LYTHRUM SALICARIA*, L.—This plant has acquired, through Darwin's numerous and laborious experiments (158), so important

a place in the question of the origin of species, that its fertilisation by insects in the wild state also deserves our special attention. I shall recapitulate first the peculiarities of its flower, next the results of Darwin's experiments, and finally the insect-visitors that I have observed.

The flowers, which are set in close whorls on a long spike, are almost regular, usually hexamerous but sometimes pentamerous, both forms occurring on the same spike; they have lost something of their regularity by standing not quite horizontally but directed slightly upwards. Of the five or six petals which are inserted on the edge of the cylindrical calyx-tube, 5 to 7 mm. long, the three lower (outer) are usually a little longer than the two or three



FIG. 85.—*Lythrum Salicaria*, L.

- 1.—Long-styled flower from above, after removal of one-third of the calyx, corolla, and stamens.
- 2.—Mid-styled flower, ditto.
- 3.—Short-styled flower, ditto.

a, long anthers or stigma; the stigma in Fig. 1, the anthers in 2 and 3 are coated with green pollen.

b, mid-sized ditto; the stigma in Fig. 2, the anthers in 1 and 3 are coated with yellow pollen.

c, short ditto; the stigma in Fig. 3, the anthers in 1 and 2 are coated with yellow pollen.

d, honey.

- 4.—Mid-styled flower, viewed obliquely from above and from the right side.

upper ones; the former are 7 to 11 mm. long, the latter 6 to 10 mm. When the flower is fully expanded, as, owing to the crowded arrangement, it seldom is, the upper petals stand vertically while the lower project obliquely forward; and the latter form, therefore, a rudimentary platform for insects. The irregularity in position of the stamens and pistil is of more importance; they all occupy the inferior (outer) part of the tube, so that insects cannot reach the base of the flower between them, but only above them; and their ends are bent upwards, so that the ventral surface of the insect must come in contact both with anthers and stigma. Honey is secreted by the fleshy base of the flower, and surrounds the short

stalk of the ovary and fills the space between it and the sides of the tube. Insects are attracted from a distance by the crimson spikes of flowers, and are guided on their way to the honey by the dark red colour of the inner surface of the calyx and by the dark lines in the middle of each petal. These insects are caused to perform regular cross-fertilisation by the *trimorphism* of the flowers, which forms the most remarkable feature of the plant.

In each flower the reproductive organs, which consist of one pistil and two whorls of stamens, of five or six each, are of three different lengths; the shortest are inclosed in the calyx-tube, the intermediate ones project 3 to 4 mm., and the longest 6 to 8 mm. beyond it, and either the style or one or other whorl of stamens may be the longest. All the flowers on any one plant are of the same kind, and the three forms are designated by Darwin, the Long-styled, Mid-styled, and Short-styled. Both pollen-grains and stigmatic papillæ differ according to the length of the organs which bear them. All the pollen-grains are elliptical when dry, and swell into a spherical form when moistened. The pollen-grains of the longest stamens are green, those from the middle-sized and shortest stamens are yellow. The pollen-grains vary in size also according to the length of the stamen that they come from, and there is even a slight difference in size between pollen-grains from stamens of the same length but belonging to flowers of different kinds. The following table exhibits these differences :—

Form of flower.	Relative length of stamens.	Size of dry pollen-grains in $\frac{1}{100}$ mm.		Diameter of moist pollen-grains in $\frac{1}{100}$ mm.	Colour of pollen-grains.
		Length.	Breadth.		
Long-styled .	Intermediate.	$7\frac{1}{2}$ — $8\frac{1}{2}$	$4$ — $4\frac{1}{2}$	$7$ — $7\frac{1}{2}$	Yellow.
Long-styled .	Short . . .	$7$ — $7\frac{1}{2}$	$3\frac{1}{2}$ — $4$	$6$ — $6\frac{1}{2}$	Yellow.
Mid-styled .	Long . . .	$9$ — $10$	$6$ — $7$	$9$ — $10$	Green.
Mid-styled .	Short . . .	$6$ — $7$	$3\frac{1}{2}$ — $4$	$6$	Yellow.
Short-styled .	Long . . .	$10$ — $11$	$6$ — $8$	$9\frac{1}{2}$ — $10\frac{1}{2}$	Green.
Short-styled .	Intermediate.	$7$ — $8$	$4$ — $5$	$7$ — $7\frac{1}{2}$	Yellow.

So the longest stamens have the largest pollen-grains, and the shortest the smallest.

The pollen-grains of the long stamens differ more from those of the middle-sized and short stamens than these from each other. The stigmatic papillæ in the long-styled forms are considerably longer and have their free ends farther apart than those in the mid-styled and short-styled forms, which in this respect also do not

differ so much from each other. In all these forms the stigmatic papillæ consist of long cells, whose ends are cut off as round or elliptical knobs by a narrow neck. In the long-styled flowers these cells are  $\frac{4.0-6.0}{3.00}$  mm. long, and as the part below the constriction is about twice as thick as the knob above, these knobs stand at a distance from each other equal at least to their own diameter. In the mid-styled form these papillæ are only  $\frac{3.0-5.0}{3.00}$  mm., and in the short-styled  $\frac{2.5-4.5}{3.00}$  mm. long; and in both, the knobs stand very near together, since the part of the cell below the constriction is little thicker than that above.

Now it was Darwin's great service to prove beyond question, by a long series of patient experiments, that in *Lythrum Salicaria* reproductive organs, when of different length, behave to one another like different species of the same genus in regard both to direct productiveness and the character of the offspring; and that consequently mutual barrenness, which was once thought conclusive proof of difference of species, is worthless as such, and the last barrier that was raised between species and varieties is broken down.

Now of the eighteen possible ways of fertilisation,—applying the six different kinds of pollen to the three kinds of stigmas,—those six only are fully productive in which a stigma receives pollen from a stamen of equal height. The probability that the large pollen-grains from the long stamens are only suited to the long, widely separate papillæ on the long styles (and so forth in the other cases) is thus fully confirmed by experiment. But such an adaptation, such a differentiation of the sexual parts, is only intelligible if it can be shown that under natural conditions insect-fertilisation causes the distribution of pollen to the proper stigmas; and it is clearly proved by observation that this is so.

The honey of *Lythrum Salicaria*, inclosed at the base of a tube 5 to 7 mm. long, is accessible (1) to insects which have a proboscis 5 to 7 mm. long; and (2), since the entrance to the tube is  $2\frac{1}{2}$  to 3 mm. wide, to insects whose head is small enough to be thrust partly or entirely into the tube; and (3) to insects small enough to creep down to the base of the flower.

Almost every insect, whose body along with its proboscis is at least 12 to 15 mm. long, must in sucking the honey touch the shortest organs with its proboscis, or, if this is less than 5 to 7 mm. long, with the under side of its head; the next series with a part of its ventral surface 4 to 5 mm. further back, and the third series with another part of its ventral surface the same distance behind

the last. Thus all the three kinds of stigmas will tend in time to receive pollen from stamens of their own length. If the middle-sized and longest organs were also inclosed within the tube, the proboscis or head of the insect in passing down would come in contact with all, one after the other, and cross-fertilisation could not be nearly so well restricted to its proper lines. In point of fact, the insect alighting on the middle-sized and longest organs never has occasion to touch these with its proboscis or the fore-part of its ventral surface, the parts that are to come in contact with the shortest organs; nor is the posterior part of the ventral surface which has been in contact with the longest organs, ever brought forward during the process of sucking to touch the intermediate ones. So that, as a rule, "legitimate crossing" only is performed.

In the action just described, which leads regularly to legitimate crossing, only the larger and middle-sized bees and the larger flies take part.

I have observed : (1) *Cilissa melanura*, Nyl. ♂ and ♀, wherever *Lythrum Salicaria* grows, both sucking honey and gathering pollen, and almost confining itself to this one plant. (Since its proboscis is only 3—4 mm. long, it must thrust a great part of its head, which is 2—3 mm. broad, into the tube : it then touches the shortest reproductive organs with the under surface of its head, the next with the ventral surface of its thorax, and the longest with the ventral surface of its abdomen ; so that its dimensions suit the flower, just as well as the flower must suit it, for the insect to confine its visits so exclusively to it. I have only found one exception to this exclusiveness, for I once found a male of *Cilissa melanura* sucking honey on *Thrinacia hirta*, D.C.) ; (2) *Saropoda rotundata*, Pz. ♀ ♂, frequently (body without proboscis 10—11 mm., proboscis 9 mm. long) ; (3) *Apis mellifica*, L. ♀ (body without proboscis 11—13 mm., proboscis 6 mm. long) ; (4) *Bombus terrestris*, L. ♀ (body 12—16 mm., proboscis 7—9 mm.) ; (5) *B. agrorum*, F. ♀ (body 10—13 mm., proboscis 9—11 mm.) ; (6) *B. silvarum*, L. ♀ (body 10—12 mm., proboscis 10—12 mm.). All the humble-bees were frequent, and, like Nos. 2 and 3, sucking honey only ; (7) *Megachile centuncularis*, L. ♂ (body 10 mm., proboscis 6—7 mm.), also sucking honey. The last six species, as the annexed measurements show, have all tongues long enough to reach the honey by thrusting in the tongue alone ; they all therefore touched the shortest organs with their tongues, the next series with the lower surface of the head, and the longest with a part of the ventral surface of the body 4—5 mm. further back. The hive-bee must, in full-sized flowers, have thrust the extremity of its head 1 mm. deep into the calyx-tube.

Besides these bees, which deserve to be placed in the first rank as legitimate fertilisers, the *Loosestrife* is visited by a number of long-tongued flies, especially *Rhingia rostrata*. This fly, standing on one or more of the petals, after gently rubbing its forefeet together, and brushing its tongue and head with them, stretches its proboscis out to a length of 11—12 mm., and thrusts it down into the flower, letting it remain there from six to ten seconds. Immediately after withdrawing it from the tube, it usually manipulates one of the anthers with its

labellæ for a short time (one to two seconds) in order to add to the liquid non-nitrogenous food some solid nitrogenous matter in the shape of pollen-grains. In inserting its proboscis into the tube, the conical prolongation of the head comes in contact with the middle-sized reproductive organs, while the proboscis itself touches the shortest; the longest organs come at times in contact with the ventral surface of the fly, but very often fail to do so; and so this fly, as a rule, only performs two-thirds of the legitimate work of fertilisation. Two other Syrphidæ, *Helophilus pendulus*, L., and *H. trivittatus*, F. (proboscis 6—7 mm. long), alight upon the longest reproductive organs, and fertilise all three kinds of flowers legitimately; so also does *Volucella plumata*, L., whose proboscis is 7—8 mm. long. Several smaller Syrphidæ, whose proboscis is too short to reach the honey, viz. *Syritta pipiens*, L. (proboscis 3 mm.), *Syrphus balteatus*, Deg. (2 mm.), and *Melithreptus tæniatus*, Mgn., feed on the pollen, which they may chance to carry to the stigmas; but they are as likely to perform illegitimate as legitimate fertilisation. The same holds good of *Haliectus cylindricus*, F. ♀, which has likewise too short a proboscis to reach the honey, and only collects pollen on this flower; and also of some very small insects, *Nanophyes lythri*, F., *Meligethes*, and *Thrips*, which creep down into the tube, and of a species of *Capsus* which runs about indiscriminately on the leaves and also on the flowers of the plant.

Two butterflies also, *Rhodocera rhamni*, L., and *Pieris rapæ*, L., are to be seen rather abundantly on the flowers of the Loosestrife. The butterfly, sitting upon one flower, thrusts its proboscis (15 mm. long) into the next; it thus touches the shortest organs regularly with its proboscis, but seldom the middle-sized ones, and the longest scarcely ever, but the middle-sized and longest organs of the flower on which it is seated come in contact with the ventral surface of its body.

In the following list, those insect-visitors which regularly accomplish cross-fertilisation in its three forms are marked with (!); those which as a rule only effect one or two forms of crossing are printed without special mark; and those which only occasionally fertilise the plant, and perform illegitimate as often as legitimate fertilisation, are placed in parentheses.

A. Hymenoptera—*Apidæ*: (1) *Cilissa melanura*, Nyl. ♂ ♀ ! s. and c.p., ab.; (2) *Saropoda rotundata*, Pz. ♂ ♀ ! s., not rare; (3) *Apis mellifica*, L. ♀ ! s.; (4) *B. terrestris*, L. ♀ ! s.; (5) *B. agrorum*, F. ♀ ! s.; (6) *B. silvarum*, L. ♀ ! s.; (7) *Megachile centuncularis*, L. ♂ ! s.; (8) (*Haliectus minutissimus*, K. ♀, s.); (9) (*H. cylindricus*, F. ♀, c.p.). B. Diptera—*Syrphidæ*: (10) *Rhingia rostrata*, L., s. and c.p.; (11) *Helophilus pendulus*, L. ! s.; (12) *H. trivittatus*, F. ! s.; (13) *Volucella plumata*, L. ! s.; (14) (*Syritta pipiens*, L., f.p.); (15) (*Syrphus balteatus*, Deg., f.p.); (16) (*Melithreptus tæniatus*, Mgn., f.p.). C. Lepidoptera—*Rhopalocera*: (17) *Rhodocera rhamni*, L., s., ab.; (18) *Pieris rapæ*, L., s., ab. D. Coleoptera—(a) *Curculionidæ*: (19) (*Nanophyes lythri*, F.); (b) *Nitidulidæ*: (20) (*Meligethes*). E. Thysanoptera—(21) (*Thrips*). F. Hemiptera—(22) (*Capsus*). See also No. 590, II.

*Lythrum Graefferi*, Ten., is, like *L. Salicaria*, trimorphic; *L. thymifolia*, L., is dimorphic, and *L. hyssopifolia*, L., homomorphic (Darwin, No. 154).

Besides *Lythrum*, *Nescea*, Commers., and *Lagerstræmia*, L., have

trimorphic species; *Pemphis*, Forst., has dimorphic species (Kuhn, No. 399, Darwin, No. 167, 2nd ed.). Koehne mentions twenty-one heterostylic and 340 homostylic species of *Lythrum*; according to him, *L. thymifolia* is not heterostylic (394). *Pemphis acidula*, Forst., and some species of *Rotala*,<sup>1</sup> L., and *Nesaea* are clearly heterostylic and dimorphic.

*Ammannia latifolia*, L., has cleistogamic flowers (394).

*Cuphea silenoides*, Nees, *C. floribunda*, Lehm., and *C. Melvillei* Lindl., according to Treviranus, fertilise themselves before the flower opens (742).

#### ORD. ONAGRARIÆ.

166. *EPILOBIUM ANGUSTIFOLIUM*, L.—The markedly proterandrous flower was thoroughly discussed by Sprengel, who noticed humble-bees as its fertilisers. The bright crimson racemes, a foot long, are very conspicuous. The honey is secreted by the green, fleshy, upper surface of the ovary, and is easily accessible to insects and yet well sheltered from rain. The expanded lower ends of the filaments form a hollow cone, which incloses the base of the style and the surrounding honey; where the style issues at the apex of this cone, hairs upon the style prevent the entrance of raindrops, while insects easily gain access between the filaments.

In young flowers the stamens, covered above with pollen, project forwards as an alighting-place for insects, while the style is still short and bent downwards, with its stigmas folded together; in older flowers, the empty stamens are bent downwards, and the style, greatly increased in length, projects forwards with its four stigmas outspread and recurved. Alighting, sucking, and pollen-collecting are thus all made easy, cross-fertilisation in case of insects-visits is insured, and self-fertilisation rendered impossible. In fine weather, sufficient insect-visits are always insured by the conspicuous colour, size, and grouping of the flowers, and by the abundance and accessible position of the pollen and honey.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, s., very ab.; (2) *Bombus lapidarius*, L. ♀ ♀; (3) *B. pratorum*, L. ♀ ♀ ♂; (4) *B. terrestris*, L. ♀ ♀ ♂; (5) *B. confusus*, Schenck, ♀, all ab., s.; (6) *B. agrorum*, F. ♀ ♀ ♂, very ab., s.; (7) *B. (Apathus) campestris*, Pz. ♂, s.; (8) *Sphcodes gibbus*, L. ♀, s.; (9) *Nomada Roberjeotiana*, Pz. ♀, s.; (10) *N. Jacobae*, Pz. ♂, s.; (b) *Sphégidae*: (11) *Cerceris nasuta*, Latr.; (12) *Crabro alatus*, Pz.; (13) *Ammophila sabulosa*, L.; (c) *Tenthredinidae*: (14) *Tenthredo serophulariae*, L., all sucking. B. Diptera—(a) *Empidae*: (15) *Empis rustica*, Fallen;

<sup>1</sup> Vide Bentham and Hooker, *Genera Plantarum*, i. p. 776.

16, *E. livida*, L., both sucking, abundant; (17) *Syrphus ribesii*, L., f. p. D. Lepidoptera—*Sphinxes*: (18) *Ino statice*, L., s. See also No. 590, II., and No. 609.

*Epilobium Fleischeri*, Hochst. (*E. denticulatum*, Ulender), is visited by numerous humble-bees. It is sometimes homogametic, sometimes proterandrous, sometimes proterogynous, and the short style always occupies the same position below the stamens. Cross fertilisation is generally insured, but self-fertilisation is not quite excluded (No. 609, fig. 82).

Insect-visitors of *E. Dodonæi*, Vill., *E. organifolium*, Lam., and *E. montanum*, L. (*E. collinum*, Gmel.), are enumerated in *Das Alpenblumen*.

167. *EPILOBIUM PARVIFLORUM*, Schreber.—In regard to the power of attracting insects and the possibility of self-fertilisation two species of the same genus could scarcely stand in greater

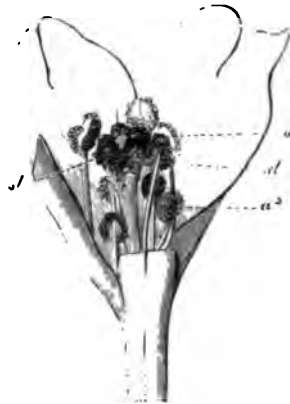


FIG. 86.—*Epilobium parviflorum*, Schreber.

Flower, in side view, the greater part of the calyx and ovary and the two anterior petals have been removed.

st. stigma; a', longer stamens; a'', shorter ditto.

contrast to each other than *Epilobium parviflorum* and *E. angustifolium*; for the solitary, pale-red flowers of the former species are easily overlooked even by the practised eye, and generally expect their honey to no purpose, receiving insect-visits only exceptional. Accordingly self-fertilisation is a regular occurrence.

The honey is secreted by the upper surface of the ovary and is lodged round the base of the style; it is sheltered from rain and so much by the stamens as by a ring of hairs projecting inward from the petals. Stamens and stigmas ripen together. The fe

shorter stamens are set apart for cross-fertilisation, as they stand below the stigmas and are touched without fail by honey-seeking insects. The stigmas, standing in the centre of the narrow flower, must be touched first by an insect-visitor. The four longer stamens are concerned in self-fertilisation, and stand close round the stigmas, which are provided with long stigmatic papillæ on their outer as well as on their inner sides. We must suppose that in case of insect-visits the pollen brought from without predominates in its action over the pollen belonging to the flower. In spite of frequent watching, I have only observed *Pieris rapæ* and a *Meligethes* sucking honey on this plant.

168. *EPILOBIUM ORIGANIFOLIUM*, Lam.—This Alpine species is comparable in many respects to *E. parviflorum*. The flowers are small, tubular, and inconspicuous; the style is unbranched, and stigmatic papillæ form a uniform covering for its upper end. The stigma is fully ripe on the opening of the flower, the stamens reach maturity a little later. The upper whorl of stamens performs self-fertilisation regularly, while the lower whorl provides for occasional crossing. *Argynnis Pales* was observed sucking several flowers.

*Epilobium hirsutum*, L.—The flowers of this species, whose rosy corolla expands to a diameter of 25 to 30 mm., are, taken

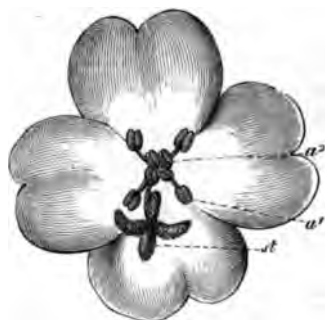


FIG. 87.—*Epilobium hirsutum*, L.

singly, still more conspicuous than those of *E. angustifolium*; but the latter is rendered the more conspicuous of the two by the aggregation of more numerous flowers. I have had no opportunity of watching *E. hirsutum* in the right places at the right time; but from the arrangement of its flowers, as well as from its less striking appearance, it is probable that its insect-visitors are not so

numerous as those of *E. angustifolium*. For while in the latter species distinct proterandrous dichogamy and the change in position of the reproductive organs have quite excluded self-fertilisation, it remains possible in *E. hirsutum*. The stigmas here ripen simultaneously with the anthers: cross-fertilisation is insured in case of insect-visits by the more prominent position of the stigmas; but in absence of insects the stigmas curl backwards, and come in contact with the pollen of the longer stamens.

*Epilobium alpinum*, L., produces seed by self-fertilisation in the absence of insects (Areal, No. 17).

A review of the foregoing species of *Epilobium* brings us to the same result that a comparison of the *Geraniums*, *Polygonums*, *Alnaceæ*, etc., leads us to, and confirms the view that no general deduction for a whole genus can be drawn from the floral mechanism of a single species, but that each new species must be investigated afresh. When Delpino (1754) characterised the genus *Epilobium* as dichogamic and fertilised exclusively by bees, this description may perhaps have been true of some particular species that I am unacquainted with; but it certainly cannot be sustained for the whole genus.

160. *ENOTHERA BIENNIS*, L.—The structure of this flower was minutely explained by Sprengel. The flower opens and is most strongly odorous in the evening, and seems to have adapted itself in this way to crepuscular and nocturnal *Lepidoptera*. But not only is the pollen exposed to bees and flies, as in the nocturnal flowers hitherto described, but the honey also is accessible to long-tongued bees. The colour of the flower is not white, as most nocturnal flowers are, but bright yellow, and the flower remains open or partially open during the day; so that it is probably more correct to look upon the flower as adapted simultaneously for bees and nocturnal *Lepidoptera*.

Visitors: A. *Lepidoptera*—*Sphinges*: (1) *Macroglossa stellatarum*, L., towards evening, sucking without settling on the flower. This species was probably observed by Sprengel also (No. 702, p. 221). B. *Hymenoptera*—*Apide*: (2) *Bombus lapidarius*, L. ♀; (3) *B. silvarum*, L. ♀; (4) *B. agrorum*, F. ♀, all three sucking; (5) *Apis mellifica*, L. ♂, ♀, and c.p.; (6) *Colletes Daviesiana*, K. ♀, c.p.; (7) *Panurgus calcaratus*, Scop. ♀ ♂, dusting itself with the pollen. C. *Diptera*—*Syrphida*: (8) *Eristalis tenax*, L.; (9) *E. arbustorum*, L.; (10) *E. nemorum*, L.; all three feeding on pollen, very abundant.

*Enothera sinuata*, Mx.—Trelease saw this flower visited by Ruby-throated Humming-birds (731).

*Oenothera tenella*, Bert. (*Godetia Cavanillesii*, Spach.), in the central province of Chili, produces cleistogamic flowers in spring.<sup>1</sup>

*Fuchsia*, L., is visited in New Zealand by Nectarinidæ (*Anthornis melanura*); and in North America by Ruby-throated Humming-birds (Potts, No. 652A, and Trelease, No. 731).

*Lopezia coronata*, Andr.—The floral mechanism of this plant is described and figured by Hildebrand (346). In each flower there is present one perfect stamen; a second, standing immediately below, is reduced to a spatulate leaf, whose two halves fold upwards, and in the first stage, projecting horizontally from the flower, inclose the anther of the perfect stamen. The stalk of the spatulate leaf has an elastic tension downwards, the filament of the stamen an elastic tension upwards; so when an insect alights on the projecting spoon-shaped blade, as the only convenient spot from which to reach two drops of honey that seem to rest upon a knee-shaped bend in the upper petals, the leaf springs downwards, and the stamen is set free and flies upwards, dusting the lower surface of the insect with pollen. When the stamen has thus served its purpose, it gradually curves upwards out of the flower; and the style which was hitherto undeveloped grows gradually out of the flower in a horizontal direction, so as to form another alighting-place. Self-fertilisation is rendered impossible by this marked proterandry. I have frequently seen the whole process performed in my room by the house-fly (*Musca domestica*, L.), and by the common gnat (*Culex pipiens*, L.); and also at an open window by the hive-bee.

What seem to be drops of honey on the two upper petals are in reality dry, shining bodies which deceive the flies as well as us. *Lopezia coronata* is therefore a deceptive flower like *Parnassia*; but like the latter, also, it possesses real nectaries in addition,—two yellow pits at the base of the two stamens, the functional and the abortive (Delpino, No. 178).

*Lopezia racemosa*, Cav., seems, from Ogle's description (No. 631), to agree fully in the structure of its flower with *L. coronata*.

*Lopezia miniata*, D.C., is likewise markedly proterandrous; but its stamen is not irritable, and does not lie inclosed by the spoon-shaped staminode, but stands above it (Hildebrand, No. 356).

170. *CIRCÆA LUTETIANA*, L.—This plant is fertilised much in the same way as *Veronica Chamædrys*, L., in spite of the small

<sup>1</sup> Philippi, *Bot. Zeit.* 1870, pp. 104-106.

back of the insect-visitor. Delpino has observed humble-bees and *Xylocopa violacea* accomplishing cross-fertilisation in this manner. (172).

In *Passiflora racemosa*, Brot. (*P. princeps*, Lodd.), the tube is divided by rings of hairs into three chambers, the lowest of which contains the honey. From the size of the flowers, and their rich store of honey, Delpino imagines that humming-birds are the fertilisers; and he supposes that the triple fence serves to keep away less intelligent visitors (178).

My brother Fritz Müller has observed in his garden at Itajahy that some *Passifloræ* are fertilised exclusively or chiefly by humming-birds; but he is convinced that abundance of honey is no proof of the flower being visited by humming-birds, for one species in his garden, which is very diligently visited by them, contains no honey and is odourless, while another smaller white species flowering in Itajahy, in spite of great abundance of honey and a pleasant scent, is never visited by humming-birds. The numerous coronæ, projecting ledges, etc., seem to him to be of service in detaining small insects in the lowest chamber (which often contains no honey) and keeping them caged for the humming-birds, rather than in making access to the chamber difficult for unprofitable visitors of low intelligence.

#### ORD. CUCURBITACEÆ.

171. BRYONIA DIOICA, L.—The lower part of the calyx and corolla, both in the male flowers and in the female flowers (which are only half as large) is adherent to a hemispherical cup-shaped disk, whose naked, fleshy floor secretes honey. In the male flower five irregularly formed fleshy stamens arise on the edge of this cup, and are so expanded and inclined inwards that they completely roof in the cup. Four of the anthers cohere, to form two pairs; the fifth is free on both sides. Thus the honey-holding cup has three narrow lateral entrances each placed between two stamens and fringed with long hairs; and also an entrance from above in the midst of the upper ends of the stamens. The anthers form narrow ridges on the broad stamens, and the long, narrow slits by which they dehisce are so bent that the greater part of each faces one of the lateral openings, while the uppermost portion looks directly upwards. A honey-seeking insect alighting in the middle of the flower may thrust its proboscis down in the midst of all the stamens, or approaching from the side it may reach the

opposite to that which the anther touches at the same time ; and so cross-fertilisation may result if the insect has come from another flower.

In absence of insects, the flowers mostly wither without self-fertilisation taking place, as I have observed in specimens in my room. I have found a few flowers in which the stigma, instead of being directed obliquely downwards between the two stamens, was in contact with one of them from the beginning.

The only visitors that I have seen are small flies which behaved in the manner described. I have collected (a) *Syrphidæ* : (1) *Baccha elongata*, F. ; (2) *Ascia podagrica*, F. ; (3) *Melanostoma mellina*, L. ; (b) *Muscidæ* : (4) *Anthomyia* sp., with yellow abdomen. Several other small *Muscidæ* and *Syrphidæ* escaped me.

On a bunch of *Circæa lutetiana* which I kept in a glass of water in my room, I found a great number of house-flies : (5) *Musca domestica*, L., sucking honey and fertilising the flowers.

#### ORD. *LOASEÆ*.

*Cajophora lateritia* is distinctly proterandrous, according to Delpino. In the first period the anthers, which lie in five bundles in the hollow and outspread petals, rise up one by one, bend inwards towards the middle of the flower, and pass back into their old position after giving up their pollen to insects. With these five bundles there alternate five groups each containing five metamorphosed stamens ; in each of these latter groups the three outermost staminodes cohere and form in their expanded base a honey-receptacle, while the two inner ones incline as stiff rods towards the middle of the flower, and their bases, expanded and fringed with hairs, give shelter to the honey. After the anthers have all withered, the pistil grows up and unfolds its stigma.

In the first period the insects cling to the central tuft of stamens ; in the second, to the stiff metamorphosed protective staminodes. The fertilisers seem to be bees, according to Delpino (177). This is in direct contradiction to Treviranus' view, that the flowers of *Cajophora* are self-fertilising (742).

#### ORD. *PASSIFLOREÆ*.

*Passiflora cærulea*, L., was thoroughly described by Sprengel, who recognised it as a proterandrous form in which the anthers in the first stage, and stigma in the second, came in contact with the

c.p. only ; (5) *H. sexnotatus*, K. ♀, c.p. only ; (6) *Cœlixys simplex*, Nyl. ♀, s. ; (7) *Apis mellifica*, L. ♀, c.p. ; (b) *Sphegidae* : (8) *Gorytes mystaceus*, L., freq., s. ; (9) *Ammophila sabulosa*, L., freq., s. ; (c) *Vespidae* : (10) *Eumenes pomiformis*, L. ♂ ; (11) *Odynerus parietum*, L. ♀, both sucking. B. Coleoptera — *Malacodermata* : (12) *Dasytes* sp., only on the male flowers, f.p. C. Lepidoptera — *Rhopalocera* : (13) *Pieris napi*, L., s. See also No. 590, II.

The flowers of a species of *Trianosperma* in South Brazil are visited, according to Fritz Müller, very abundantly all day long by *Apis mellifica* and species of *Melipona*, although they are scentless, greenish, quite inconspicuous, and to a great extent hidden by foliage (597).

#### ORD. UMBELLIFERÆ.

The general phenomena of pollination in Umbelliferæ have been already so clearly and thoroughly described by Sprengel, that I may confine myself to a short account of the most important peculiarities. The main features of the flowers are : firstly, the open situation of the honey, making it accessible to even the most short-lipped insects ; and secondly, the union of many flowers in one head, making them not only more conspicuous, but also permitting them to be more quickly searched and fertilised. *Cornus* shares both of these characters with the Umbelliferæ, but in a much less perfect form.

In most Umbellifers the honey is rendered even more accessible than in *Cornus*, by the secreting disk being more convex and cushion-shaped, and by the stamens spreading further apart. The close association of many flowers is more perfectly attained in Umbelliferæ than in *Cornus*, far more numerous flowers uniting in one close-set surface, so that a visitor quickly traverses the whole ; and the florets are differentiated in the service of the community, those in the centre being condensed, and those towards the edges more expanded, rendering the whole more conspicuous.

As a further advantage comes proterandrous dichogamy, often developed to such a degree that all the florets of one whole inflorescence only protrude their styles and develop stigmas after the shedding of the pollen : so that in the first period of flowering a whole community dusts with pollen the insects that visit it, and in the second, exposes its stigmas to be dusted in return. So cross-fertilisation of separate inflorescences always takes place, and the impossibility of self-fertilisation is still further assured. Hence it happens that in many Umbellifers (e.g. *Myrrhis*) towards the end of the season only male flowers are produced, which furnish pollen

for the last of the androgynous flowers, now in their second or female stage.

*Hydrocotyle americana* is visited in Kew by minute flies (Henslow, 330).

*Hydrocotyle vulgaris*, L.—The exceedingly inconspicuous flowers fertilise themselves. I have not yet seen them visited by insects (590, 1.).

172. *ERYNGIUM CAMPESTRE*, L. (Thuringia).—As in all other Umbellifers, the upper surface of the ovary secretes and lodges the

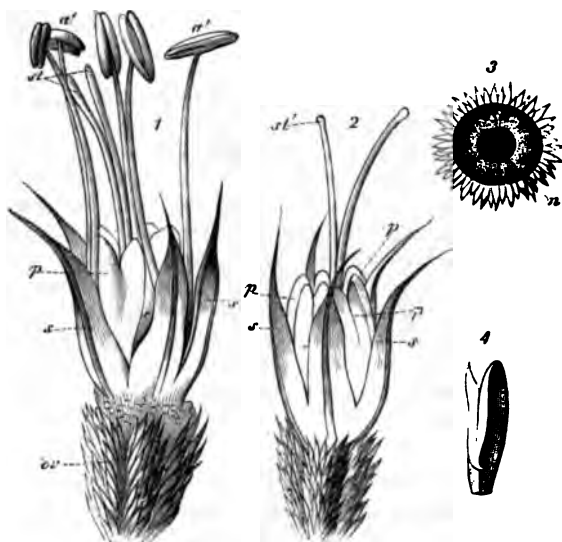


FIG. 90.—*Eryngium campestre*, L.

- 1.—Flower, in first (male) stage.
  - 2.—Ditto, in second (female) stage.
  - 3.—Ditto, after removal of sepals, petals, and styles. n, nectaries.
  - 4.—Petal, seen from within.
- (Letters as in Fig. 91).

honey: but the honey-gland here does not form, as usual, a swollen cushion covering the whole surface of the ovary, but a hollow rounded disk five-sided in outline, and surrounded by a ten-lobed rough wall of tiny (accumbent) bristles. The five equal-sized petals stand stiff and upright, with nearly the whole of their upper halves folded inwards: they stand about 3 mm. high, and are overtopped by the stiff, bristle-like sepals which alternate with them: the equally stiff and bristle-like bracts protrude still further. So the honey is accessible only to insects which have a proboscis at

least 3 mm. long, or are strong enough to push apart the floral organs which protect it. Accordingly, in connection with the fully developed proterandry, cross-fertilisation alone, as in all other Umbellifers, can take place. *Eryngium* shares only slightly in that special advantage which Umbellifers in general possess from having their flowers massed together in one surface, for the bristle-like bracts render it difficult for the insects to go creeping about the umbel. This disadvantage is somewhat atoned for by the richer secretion and better protection of the honey. Hence, in spite of the prickly flowers, insect-visits are by no means scarce, but in sunny weather we see the plant abundantly visited by wasps and flies, bees coming in much smaller numbers. I have observed as visitors and fertilisers:—

A. Hymenoptera—(a) *Sphegidae*: (1) *Cerceris albofasciata*, Dlb., scarce; (2) *C. labiata*, F., ab.; (3) *G. nasuta*, Kl., ab.; (4) *C. variabilis*, Schr., not rare; (5) *Philanthus triangulum*, F.; (6) *Ammophila sabulosa*, L., ab.; (7) *Tiphia femorata*, F.; (8) *Priocnemis bipunctatus*, F. ♀; (b) *Vespidae*: (9) *Odynerus parietum*, L. ♀; (10) *Polistes gallica*, L., and var. *diadema*, very ab., almost always to be found in sunny weather; (c) *Chrysidæ*: (11) *Chrysis* sp., all sucking; (d) *Apidae*: (12) *Nomada Roberjeotiana*, Pz. ♀; (13) *Andrena Rosæ*, Pz. ♀; (14) *Halictus cylindricus*, F. ♂; (15) *H. longulus*, Sm. ♂; (16) *Apis mellifica*, L. ♂; all only sucking. B. Diptera—(a) *Syrphidae*: (17) *Eristalis tenax*, L.; (18) *E. arbustorum*, L.; (19) *E. nemorum*, L.; (20) *Helophilus florens*, L.; all four abundant; (b) *Muscidae*: (21) *Lucilia Cæsar*, L.; (22) *Sarcophaga carnaria*, L.; (23) *Echinomyia fera*, L.; (24) species of *Anthomyia*, all sucking.

173. *ASTRANTIA MAJOR*, L.—In *Astrantia major*, the special advantages which most of the other forms develop so fully, and resemble each other so much in, are very little developed.

The umbels are simple, their florets form no close-packed surface, the petals remain rolled up in the middle of the flower, and while they thus protect the honey from rain, they make it less accessible and the flowers less conspicuous. Although the last objection is to some extent removed by the bright white bracts, insect-visits are less abundant than to most other forms of this order. I have noted the following in my garden at Lippstadt:—

A. Hymenoptera—*Apidae*: (1) *Andrena albicus*, K. ♂; (2) *Prosopis signata*, Pz. ♂; (3) *Pr. armillata*, Nyl. ♂, all three sucking. B. Diptera—(a) *Syrphidae*: (4) *Eristalis arbustorum*, L., f.p. and l.h.; (b) *Muscidae*: (5) *Lucilia cornicina*, F., l.h.; (6) *Miltogramma punctata*, Mgn. C. Coleoptera—*Dermestidae*: (7) *Anthrenus pimpinellæ*, F. On the Alps I have found the plant visited by seven species of Coleoptera, three Diptera, two Hymenoptera, and one butterfly (609).

Every inflorescence bears, besides the proterandrous, androgynous flowers, numerous male flowers which mostly develop later, and are of obvious service in this marked case of proterandry in fertilising the last of the androgynous flowers.

*Astrantia minor*, L., is both andromonœcious and androdicœcious. The plant bears as a rule only one umbel, which usually consists of male flowers surrounded by hermaphrodite flowers; the weaker plants usually bear an umbel consisting only of male flowers.

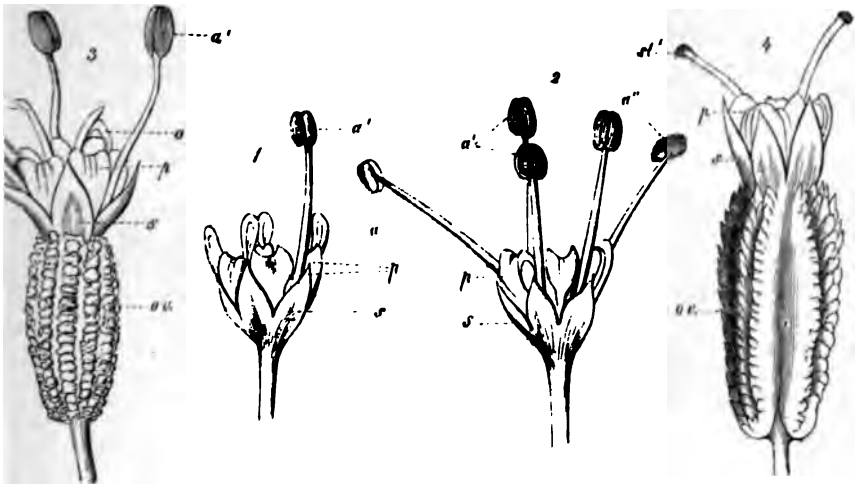


FIG. 91.—*Astrantia major*, L.

1.—Male flower beginning to expand. One stamen has risen up, but its anther has not yet dehiscent; the other four are still bent down within the flower.

2.—Male flower at the middle of its flowering-period. All five stamens are erect; two anthers have dehiscent and are coated with pollen.

3.—Hermaphrodite flower beginning to expand. Two anthers are erect, but still closed; the others are still bent down within the flower. The styles protrude, but their stigmas are not yet developed.

4.—Hermaphrodite flower in its second (female) stage. All the stamens have disappeared; the styles have elongated, and their stigmas are mature.

o, ovary; s, sepal; p, petal; a, anther, still bent down within the flower; a', ditto, erect; a'', ditto, dehiscent; st, stigma, immature; st', ditto, mature.

In regard to the distribution of the sexes, the condition in *Astrantia minor* is almost the same as in *Veratrum album*, with this exception, that in *Astrantia minor* no plants occur bearing only hermaphrodite flowers. *Veratrum album* exhibits the passage from proterandrous androgyny through andromonœcism to androdicœcism; *Astrantia minor*, with similarly proterandrous hermaphrodite flowers, shows only the passage from andromonœcism to androdicœcism (609).

*Sanicula europæa*, L., is andromonœcious. Each umbel contains one to three proterandrous hermaphrodite flowers, surrounded by ten to twenty male flowers which develop later. Both kinds resemble those of *Astrantia major* in structure (590, 1.).

174. *CONIUM MACULATUM*, L.—The adjoining figures serve to illustrate a peculiarity of the Umbellifers not well displayed in the other figures, namely the very slow and gradual development of the flowers, at first wholly male, and later wholly female.

Fig. 1 represents a flower beginning to expand, but still far below its full size. The anther  $a^1$  has dehiscent and is covered with pollen;  $a^2$  is on the point of dehiscence; the other three are not



FIG. 92.—*Conium maculatum*, L.

- 1.—Flower at the commencement of its first (male) stage.
- 2.—Ditto, in the middle of its male stage.
- 3.—Ditto, in its second (female) stage.

yet ripe;  $a^3$  is more advanced than  $a^4$ ; and  $a^5$ , the most backward, is still curled inwards: no trace of styles is yet to be seen. Each anther stands at a distance of two-fifths of the circumference from the preceding one. The second figure shows a slightly older and full-sized flower, in the middle of its male period. The anther  $a^1$  is empty and withered;  $a^2$  is half shrivelled and has still a slight dusting of pollen;  $a^3$  has just dehiscent and is fully coated with pollen;  $a^4$  is on the point of dehiscing,—it opened while the drawing was being made;  $a^5$  is still closed. The styles are still short and bent inwards with undeveloped stigmas. Lastly, the third figure shows a flower in its second stage: the anthers have fallen off; the styles have raised themselves erect; a stigmatic knob has been developed on the end of each style.

Even this notoriously poisonous plant receives abundance of insect-visitors who greedily lick up its honey.

Visitors: A. Diptera—(a) *Stratiomyidae*: (1) *Sargus cuprarius*, L.; (b) *Muscidae*: (2) *Calliphora vomitoria*, L.; (3) *Lucilia cornicina*, F.; (4) *Scatophaga stercoraria*, L.; (5) *Sepsis* sp. B. Coleoptera—(a) *Nitidulidae*: (6) *Meligethes*, ab.; (b) *Dermestidae*: (7) *Anthrenus pimpinellæ*, F.; (c) *Lamellicornia*: (8) *Trichius fasciatus*, L. C. Hymenoptera—(a) *Tenthredinidae*: (9) *Nematus vittatus*, L.; (10) Several undetermined species of *Tenthredo*; (b) *Ichneumonidae*: (11) Various species; (c) *Sphegidae*: (12) *Pompilus trivialis*, Kl. ♀; (d) *Apidae*: (13) *Andrena lepida*, Schenck, ♂. See also No. 590, I.

175. *BUPLEURUM FALCATUM*, L. (Thuringia).—I have found the dull-yellow flowers visited only by flies and Hymenoptera.

Visitors: A. Diptera—(a) *Syrphidae*: (1) *Syritta pipiens*, L., very ab., s. and f.p.; (2) *Eristalis arbustorum*, L., s.; (3) *Pipizella annulata*, Macq., s.; (b) *Bombylidae*: (4) *Anthrax flava*, Hffagg., s. B. Hymenoptera—(a) *Tenthredinidae*: (5) *Hylotoma rosarum*, F., s.; (b) *Vespidae*: (6) *Polistes gallica*, L., and var. *diadema*, s.; (c) *Ichneumonidae*: (7) Various species, s.; (d) *Apidae*: (8) *Halictus interruptus*, Pz. ♂, s. See also No. 590, I.

176. *CARUM (PETROSELINUM) SATIVUM*, L.—The visitors are chiefly flies.

A. Diptera—(a) *Syrphidae*: (1) *Eristalis arbustorum*, L.; (2) *E. sepulcralis*, L.; (3) *Helophilus florens*, L.; (4) *Syritta pipiens*, L.; (5) *Xanthogrammia citrofasciata*, Deg.; (b) *Muscidae*: (6) *Lucilia cornicina*, F.; (7) *Cyrtoneura simplex*, Loew (determined by Herr Winnertz); (8) *Sarcophaga carnaria*, L. B. Hymenoptera—*Apidae*: (9) *Sphcodes gibbus*, L. ♂, s. See also No. 590, I.

177. *CARUM CARUI*, L.:—

Visitors: A. Diptera—(a) *Stratiomyidae*: (1) *Stratiomys longicornis*, F.; (2) *Chrysomyia formosa*, Scop.; (b) *Syrphidae*: (3) *Chrysotoxum festivum*, L.; (4) *Pipizella virens*, F.; (5) *Melanostoma mellina*, L.; (6) *Pyrophæna* sp., s.; (7) *Syrphus ribesii*, L., s.; (8) *Platycheirus peltatus*, Mgn.; (9) *Melithreptus tæniatus*, Mgn.; (10) *Eristalis arbustorum*, L.; (11) *E. horticola*, Deg.; (12) *E. æneus*, Scop.; (13) *Helophilus florens*, L., very ab.; (14) *H. pendulus*, L.; (15) *Syritta pipiens*, L.; (c) *Muscidae*: (16) *Gymnosoma rotundata*, L.; (17) *Echinomyia fera*, L.; (18) *Zophomyia tremula*, Scop.; (19) *Sarcophaga carnaria*, L., and *albiceps*, Mgn.; (d) *Bibionidae*: (20) *Bibio hortulanus*, F.; (e) *Tipulidae*: (21) *Tipula*, l.h. B. Coleoptera—(a) *Curculionidae*: (22) *Bruchus*, freq.; (23) *Phyllobius oblongus*, L.; (b) *Malacodermata*: (24) *Anthocomus fasciatus*, L.; (25) *Telephorus rusticus*, L.; (c) *Chrysomelidae*: (26) *Crioceris 12punctata*, L. C. Hymenoptera—(a) *Tenthredinidae*: (27) *Hylotoma femoralis*, Kl.; (28) *H. rosarum*, F.; (29) *H. cærulescens*, F.; (30) *H. enodis*, L.; (31) *Selandria serva*, L.; (32) *Athalia spinarum*, F.; (33) *Tenthredo tricineta*, F.; (34) *T. bifasciata*, L., etc.; (35) *Dolerus eglanteriæ*, F.; (36) *Cimex sericea*, L.; (37) *Cephus troglodytes*, L.; (b) *Ichneumonidae*: (38) Numerous species; (c) *Sphegidae*: (39) *Cemonus unicolor*, F., freq.; (40) *Gorytes campestris*, L. ♂; (41) *Crabro lapidarius*, Pz. ♀; (42) *Cr. pterotus*, F. ♂; (43) *Cr. vagabundus*, Pz. ♀; (d) *Apidae*: (44) *Prosopis brevicornis*,

Nyl. ♂; (45) *P. communis*, Nyl. ♂; (46) *Halictus maculatus*, Smith, ♀, s., freq.; (47) *H. sexnotatus*, K. ♀, c.p.; (48) *H. albipes*, F. ♀, c.p.; (49) *Andrena nigroaenea*, K. ♀, s.; (50) *A. albicans*, K. ♀ ♂, s.; (51) *A. parvula*, K., s. and c.p.; (52) *A. fulvicrus*, K. ♀, s.; (53) *A. nana*, K. ♂, s., and *A. minutula*, K. ♀, s. D. Lepidoptera—*Tineidae*: (54) *Adela*, s. E. Neuroptera—(55) *Sialis lutaria*, L. See also No. 590, 1., and No. 609.

### 178. SIUM LATIFOLIUM, L. :—

A. Diptera—(a) *Empidæ*: (1) *Empis* sp.; (b) *Dolichopidæ*: (2) *Dolichopus aeneus*, Deg.; (c) *Syrphidæ*: (3) *Syrphus ribesii*, L.; (4) *Eristalis nemorum*, L.; (5) *E. arbustorum*, L.; (6) *E. aeneus*, Scop.; (7) *Syrirta pipiens*, L.; (8) *Helophilus florens*, L.; (d) *Muscidæ*: (9) *Mesembrina meridiana*, L., s.; (10) *Lucilia silvarum*, Mgn.; (11) *L. Caesar*, L.; (12) *L. cornicina*, F.; (13) *Musca corvina*, F.; (14) *Aricia incana*, Wied., freq.; (15) *Cyrtoneura simplex*, Loew; (16) *Calliphora vomitoria*, F.; (17) *Ocyptera brassicaria*, F.; (18) *Tetanocera ferruginea*, Fallen; (19) *Sepsis* sp.; (e) *Stratiomyidæ*: (20) *Stratiomys riparia*, Mgn. B. Coleoptera—(a) *Mordellidæ*: (21) *Mordella fasciata*, F.; (b) *Malacodermata*: (22) *Telephorus melanurus*, L.; (c) *Lamellicornia*: (23) *Trichius fasciatus*, L. C. Hymenoptera—(a) *Tenthredinidæ*: (24) *Selandria serva*, F.; (25) *Athalia rosæ*, L.; (26) *Tenthredo notha*, Kl.; (b) *Ichneumonidæ*: (27) Numerous species; (c) *Sphegidæ*: (28) *Crabro dives*, H. Sch. ♂; (29) *C. lapidarius*, Pz. ♂ ♀, freq.; (30) *C. pterotus*, F. ♂; (31) *C. vagus*, L. ♂. D. Hemiptera—(32) A small species of *Anthocorida*.

179. *ÆGOPodium PODAGRARIA*, L.—The flowers of this common weed are the resort of very numerous insects of various orders. I have found upon them :—

A. Diptera—(a) *Stratiomyidæ*: (1) *Stratiomys Chamæleon*, Deg.; (2) *Sargus cuprarius*, L.; (3) *Chrysomyia formosa*, Scop.; (b) *Bombylidæ*: (4) *Anthrax flava*, Mgn. (Thur.); (c) *Empidæ*: (5) *Empis livida*, L.; (6) *E. punctata*, F.; (d) *Therevidæ*: (7) *Thereva anilis*, L.; (e) *Dolichopidæ*: (8) *Gymnopternus chærophylli*, Mgn.; (f) *Syrphidæ*: (9) *Pipizella virens*, F.; (10) *Chrysogaster viduata*, F.; (11) *Ch. cœmeteriorum*, L.; (12) *Ch. chalybeata*, Mgn.; (13) *Syrphus pyrastris*, L.; (14) *S. ribesii*, L.; (15) *S. nitidicollis*, Mgn.; (16) *Melithreptus tæniatus*, Mgn.; (17) *Volucella pellucens*, L. (Tekl. B.); (18) *Eristalis arbustorum*, L.; (19) *E. nemorum*, L.; (20) *Helophilus florens*, L., ab.; (21) *Syrirta pipiens*, L., freq.; (g) *Muscidæ*: (22) *Echinomyia fera*, L.; (23) *Zophomyia tremula*, Scop.; (24) *Sarcophaga albicans*, Mgn.; (25) *Lucilia cornicina*, F.; (26) *L. silvarum*, Mgn., etc.; (27) *Musca corvina*, F.; (28) *Aricia obscurata*, Mgn.; (29) Species of *Anthomyia*; (30) *Scatophaga stercoraria*, L.; (31) *S. merdaria*, F.; (32) *Sepsis*, ab.; (h) *Tipulidæ*: (33) *Pachyrrhina histrio*, F.; (34) *P. crocata*, L. B. Coleoptera—(a) *Nitidulidæ*: (35) *Cychramus luteus*, F. (Tekl. B.); (b) *Dermestidæ*: (36) *Anthrenus pimpinellæ*, F.; (c) *Lamellicornia*: (37) *Phyllopertha horticola*, L.; (38) *Cetonia aurata*, L.; (39) *Trichius fasciatus*, L.; (d) *Elateridæ*: (40) *Agriotes aterrimus*, L.; (41) *Lacon murinus*, L.; (42) *Athous niger*, L.; (e) *Malacodermata*: (43) *Telephorus fuscus*, L.; (44) *Malachius bipustulatus*, F.; (45) *Dasytes flavipes*, F.; (46) *Trichodes apiarius*, L.; (f) *Cistelidæ*: (47) *Cistela murina*, L.; (g)

*Mordellidæ*: (48) *Anaspis rufilabris*, Gylh.; (49) *A. frontalis*, L.; (50) *Mordella fasciata*, F.; (51) *M. aculeata*, L., very ab.; (*h*) *Curculionidæ*: (52) *Spermophagus cardui*, Schh.; (*i*) *Cerambycidæ*: (53) *Pachyta octomaculata*, F. (Tekl. B.); (54) *Leptura livida*, F.; (55) *Grammoptera ruficornis*, Pz. C. Hymenoptera—(*a*) *Tenthredinidæ*: (56) *Hylotoma femoralis*, Kl.; (57) *H. rosarum*, F.; (58) *H. ustulata*, L.; (59) *H. vulgaris*, Kl.; (60) *Selandria serva*, F., ab.; (61) *Tenthredo bifasciata*, L.; (62) *T. flavicornis*, L.; (63) *T. notha*, Kl., ab.; (64) *T. atra*, Kl.; (65) *T. sp.*; (66) *Cimbex sericea*, L.; (*b*) *Ichneumonidæ*: (67) Numerous species; (*c*) *Evaniidæ*: (68) *Fœnus affectator*, F. (Thur.); (69) *F. jaculator*, F. (Thur.); (*d*) *Chrysidæ*: (70) *Hedychrum lucidulum*, F. ♂, freq.; (*e*) *Sphegidæ*: (71) *Crabro sexcinctus*, v. d. L. ♂ (Thur.); (72) *Cr. cephalotes*, H. Sch. ♂ (Thur.); (73) *Cr. lapidarius*, Pz. ♀; (74) *Cr. vagus*, L. ♀; (75) *Oxybelus bipunctatus*, Ol. ♂; (76) *O. bellicosus*, Ol. ♂, freq.; (77) *O. bellus*, Dlb. ♂; (78) *O. uniglumis*, L., very freq.; (79) *Philanthus triangulum*, F.; (80) *Cerceris variabilis*, Schr. ♀ ♂, not rare; (81) *Gorytes campestris*, L. ♀ ♂, not rare; (82) *Hoplisus laticinctus*, Lep. ♀ (Thur.); (83) *Pompilus niger*, F. ♀ (Tekl. B.); (84) *P. spissus*, Schi. ♀; (85) *P. neglectus*, Wesm. ♀ (Thur.); (86) *Myrmosa melanocephala*, F. ♀; (*f*) *Vespidæ*: (87) *Odynerus quinquefasciatus*, F. ♀; (88) *O. elegans*, F. ♀; (*g*) *Apidæ*: (89) *Prosopis communis*, Nyl. ♂; (90) *P. clypearis*, Schenck, ♂ (Thur.); (91) *Halictus albipes*, F. ♀; (92) *H. cylindricus*, F. ♀; (93) *H. minutus*, K. ♀; (94) *Andrena parvula*, K. ♀ ♂; (95) *A. albicus*, K. ♀; (96) *A. helvola*, L. ♀ ♂, c.p. and s.; (97) *A. fulvago*, Christ. ♀, c.p.; (98) *A. proxima*, K. ♀, s. and c.p.; (99) *A. albicans*, K., s.; (100) *A. pilipes*, F. ♂, s.; (101) *A. dorsata*, K. ♀, c.p.; (102) *A. fucata*, Sm. ♀, s.; (103) *Apis mellifica*, L. ♀, c.p. D. Neuroptera—(104) *Panorpa communis*, L.

180. *PIMPINELLA MAGNA*, L.—I have had very little opportunity of observing this species, and I have only noticed the following insect-visitors in Low Germany.

| *Apidæ*: (1) *Andrena parvula*, K. ♀, s. and c.p.; (2) *A. Rosæ*, Pz. ♂, s.

In the subalpine region of the Alps it usually bears only pinkish flowers (*P. magna*,  $\beta$  *rosea*, Koch = *P. rubra*, Hoppe), which circumstance may be attributed to the more intense action of light in this region. I have found the pink variety on the Alps visited by six species of beetles, seven flies, two Hymenoptera, and one butterfly (609).

#### 181. *PIMPINELLA SAXIFRAGA*, L. :—

Visitors: A. Diptera—(*a*) *Tabanidæ*: (1) *Tabanus micans*, Mgn.; (2) *Chrysops cæcutiens*, L.; (*b*) *Asilidæ*: (3) *Isopogon brevirostris*, Mgn.; (*c*) *Syrphidæ*: (4) *Syrphus nitidicollis*, Mgn.; (5) *S. pyrastris*, L.; (6) *Eristalis horticola*, Mgn.; (*d*) *Conopidæ*: (7) *Conops 4-fasciata*, Deg.; (*e*) *Tipulidæ*: (8) *Pachyrrhina crocata*, L. B. Coleoptera—(*a*) *Malacodermata*: (9) *Telephorus melanurus*, F.; (10) *Dasytes flavipes*, F. (Thur.); (*b*) *Cerambycidæ*: (11) *Pachyta octomaculata*, F., ab. (Sld.); (*c*) *Chrysomelidæ*: (12) *Clythra*

affinity between them. Two stamens and the single style project, diverging from one another, from the middle of the erect corolla; they form the platform on which an insect must stand to reach the honey, which is secreted by a fleshy ring surrounding the base of the style and is lodged in great abundance in the base of the flower. Since the style stands a little lower than the two stamens and projects a little further forward, it forms the most convenient alighting-place, and is that most usually selected. When an insect settles on it, it touches with its ventral surface the stigmatic knob at the end. As it stretches forward, and grasps with its



FIG. 88.—*Circœa lutetiana*, L.

Flower viewed obliquely from above.

*a*, ovary.

*b*, the two sepals.

*c*, the two bilobed petals, alternating with the sepals.

*d*, the two anthers.

*e*, stigma.

forefeet the bases of the two stamens, which are the only available supports, it involuntarily draws the stamens (which are very thin at their base, and therefore easily moved) inwards and downwards, so that the anthers dust the under surface of its body with pollen. Though this is apparently the simplest course which an insect can take, and that which most surely leads to cross-fertilisation, it is not the only one. The insect not unfrequently alights upon one of the stamens, and as this bends downwards it grasps the base of the same stamen and of the style with its forefeet. If the style now brings its stigma in contact with the ventral surface of the *insect*, as is usually, but not always, the case, it touches the side

opposite to that which the anther touches at the same time ; and so cross-fertilisation may result if the insect has come from another flower.

In absence of insects, the flowers mostly wither without self fertilisation taking place, as I have observed in specimens in my room. I have found a few flowers in which the stigma, instead of being directed obliquely downwards between the two stamens, was in contact with one of them from the beginning.

The only visitors that I have seen are small flies which behaved in the manner described. I have collected (a) *Syrphidæ* : (1) *Baccha elongata*, F. ; (2) *Ascia podagrica*, F. ; (3) *Melanostoma mellina*, L. ; (b) *Muscidæ* : (4) *Anthomyia* sp., with yellow abdomen. Several other small *Muscidæ* and *Syrphidæ* escaped me.

On a bunch of *Circæa lutetiana* which I kept in a glass of water in my room, I found a great number of house-flies : (5) *Musca domestica*, L., sucking honey and fertilising the flowers.

#### ORD. LOASEÆ.

*Cajophora lateritia* is distinctly proterandrous, according to Delpino. In the first period the anthers, which lie in five bundles in the hollow and outspread petals, rise up one by one, bend inwards towards the middle of the flower, and pass back into their old position after giving up their pollen to insects. With these five bundles there alternate five groups each containing five metamorphosed stamens ; in each of these latter groups the three outermost staminodes cohere and form in their expanded base a honey receptacle, while the two inner ones incline as stiff rods towards the middle of the flower, and their bases, expanded and fringed with hairs, give shelter to the honey. After the anthers have all withered, the pistil grows up and unfolds its stigma.

In the first period the insects cling to the central tuft of stamens ; in the second, to the stiff metamorphosed protective staminodes. The fertilisers seem to be bees, according to Delpino (177). This is in direct contradiction to Treviranus' view, that the flowers of *Cajophora* are self-fertilising (742).

#### ORD. PASSIFLOREÆ.

*Passiflora incarnata* L. was thoroughly described by Linnaeus, who recognised it as a proterandrous form in which the anthers in the first stage and stigma in the second came in contact with the

octomaculata, F. (Thur.); (45) *Grammoptera lurida*, F. (Tekl. B.); (46) *G. ruficornis*, F. C. Hymenoptera—(a) *Tenthredinidæ*: (47) *Hylotoma femoralis*, Kl. (Thur.); (48) *Macrophya neglecta*, Kl.; (49) *Tenthredo notha*, Kl.; (50) *T. rapæ*, Kl.; (51) *T. annulata*, F.; (52) *T. rustica*, L.; (53) *T. sp.*; (54) *Selandria serva*, F.; (55) *Athalia rosæ*, L.; (56) *Dolerus cenchris*, Htg.; (57) *Nematus vittatus*, Lep.; (58) *N. myosotidis*, F.; (b) *Ichneumonidæ*: (59) Various species; (c) *Formicidæ*: (60) Various species; (d) *Sphegidæ*: (61) *Crabro sexcinctus*, v. d. L. ♂; (62) *Cr. cephalotes*, H. Sch. ♂ (Thur.); (63) *Hoplisis laticinctus*, Lep. ♀ (Thur.); (64) *Pompilus neglectus*, Wesm. ♀ (Thur.); (65) *P. viaticus*, L. ♀; (e) *Vespidæ*: (66) *Odynerus elegans*, H. Sch. ♀ (Tekl. B.); (f) *Apidæ*: (67) *Halictus Smeathmanellus*, K. ♀; (68) *Andrena parvula*, K., s. and c.p.; (69) *A. Collinsoniana*, K. ♀; (70) *A. fucata*, Sm. ♀; (71) *Apis mellifica*, L. ♀, c.p. D. Neuroptera—(72) *Sialis lutaria*, L.; (73) *Hemerobius sp.* See also No. 590, 1.

### 186. ANTHRISCUS CEREFOLIUM, Hoffm.:—

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Eristalis arbustorum*, L.; (2) *E. nemorum*, L.; (3) *Syritta pipiens*, L.; (b) *Muscidæ*: (4) *Gymnosoma rotundata*, L.; (5) *Exorista vulgaris*, Fallen; (6) *Sarcophaga hæmarrhoa*, Meigen (determined by Herr Winnertz); (7) *S. dissimilis*, Mgn. (do.); (8) *Cyrtoneura simplex*, Loew. (do.); (9) *Anthomyia radicum*, L. (do.); (10) *Sepsis sp.*, l.h.; (c) *Bibionidæ*: (11) *Bibio hortulanus*, F. B. Coleoptera—(a) *Nitidulidæ*: (12) *Meligethes*, very ab., l.h., also pairing on the flowers; (b) *Dermestidæ*: (13) *Anthrenus pimpinellæ*, F.; (14) *A. scrophulariæ*, L., both ab., l.h.; (c) *Malacodermata*: (15) *Anthocomus fasciatus*, L.; (16) *Malachius æneus*, F.; (d) *Mordellidæ*: (17) *Anaspis frontalis*, l.h.; (c) *Cerambycidæ*: (18) *Grammoptera ruficornis*, F., l.h. C. Hymenoptera—(a) *Ichneumonidæ*: (19) Numerous species; (b) *Formicidæ*: (20) Several species; (c) *Sphegidæ*: (21) *Oxybelus uniglumis*, L., ab.; (22) *Pompilus pectinipes*, v. d. L. ♂; (23) *P. spissus*, Schi.; (d) *Apidæ*: (24) *Prosopis communis*, Nyl. ♂; (25) *P. armillata*, Nyl. ♀; (26) *Apis mellifica*, L. ♀, c.p.

### 187. CENANTHE FISTULOSA, L.:—

Visitors: A. Diptera—(a) *Stratiomyidæ*: (1) *Stratiomys Chamæleon*, Deg.; (b) *Empidæ*: (2) *Empis livida*, L.; (3) *E. rustica*, Fallen; (c) *Leptidæ*: (4) *Antherix ibis*, L.; (d) *Syrphidæ*: (5) *Syritta pipiens*, L.; (6) *Eristalis nemorum*, L.; (7) *E. arbustorum*, L.; (8) *E. sepulcralis*, L.; (9) Various species of *Lucilia*, all sucking. B. Coleoptera—*Lamellicornia*: (10) *Trichius fasciatus*, L. C. Hymenoptera—*Apidæ*: (11) *Macropis labiata*, Pz. ♂, s.; (12) *Heriades truncorum*, L. ♀, s.; (13) *Prosopis sp.* See also No. 590, 1.

### 188. CENANTHE PHELLANDRIUM, Lam.:—

Visitors: A. Diptera—(a) *Stratiomyidæ*: (1) *Odontomyia viridula*, F.; (b) *Syrphidæ*: (2) *Syritta pipiens*, L.; (3) *Eristalis arbustorum*, L., and others; (c) *Muscidæ*: (4) *Lucilia cornicina*, F.; (5) *Aricia vagans*, Fallen; (6) *Cyrtoneura curvipes*, Macq. (determined by Herr Winnertz); all sucking; (d)

*Mycetophilidæ* : (7) *Sciara* Thomæ, L. B. Coleoptera—(a) *Chrysomelidæ* : (8) *Helodes Phellandrii*, L., devouring whole umbels down to the peduncle ; (b) *Cerambycidæ* : (9) *Leptura livida*, L., ab., licking the fleshy disk ; (c) *Elateridæ* : (10) *Adrastus pallens*, Er. C. Hymenoptera—(a) *Tenthredinidæ* : (11) *Athalia rosæ*, L. ; (12) *Tenthredo* sp. ; (b) *Ichneumonidæ* : (13) various species ; (c) *Sphegidæ* : (14) *Tiphia ruficornis*, K. ; (15) *Oxybelus bipunctatus*, Ol. ♀ ; (16) *Pompilus viaticus*, L. ; (17) *P. trivialis*, Kl. ♂ ; (d) *Apidæ* : (18) *Prosopis variegata*, F. ♂ ; (19) *Sphecodes gibbus*, L. ♂. D. Lepidoptera—(20) *Vanessa C-album*, L.

189. *SILAUS PRATENSIS*, Bess.—I can only mention the following as fertilisers of this species, which I have had few opportunities of observing :—

Hymenoptera—(a) *Tenthredinidæ* : (1) *Tenthredo notha*, Kl. ; (b) *Sphegidæ* : (2) *Pompilus viaticus*, L. ♂, l.h. ; (c) *Apidæ* : (3) *Halictus longulus*, Sm. ♂, s.

#### 190. *ANGELICA SILVESTRIS*, L. :—

Visitors : A. Diptera—(a) *Syrphidæ* : (1) *Syritta pipiens*, L. ; (2) *Helophilus florens*, L. ; (3) *Eristalis pertinax*, Scop. ; (4) *Pipizella virens*, F. ; (b) *Muscidæ* : (5) *Tachina præpotens*, Mgn. (determined by Herr Winnertz) ; (6) *Echinomyia fera*, L. ; (7) *Mesembrina meridiana*, L. ; (8) *Scatophaga stercoraria*, L. ; (9) *S. merdaria*, F. ; (10) *Lucilia silvarum*, L. ; (11) *Sarcophaga* sp. B. Coleoptera—(a) *Dermestidæ* : (12) *Anthrenus pimpinellæ*, F. ; (b) *Lamellicornia* : (13) *Trichius fasciatus*, L., l.h. ; (c) *Malacodermata* : (14) *Telephorus melanurus*, L. ; (d) *Coccinellidæ* : (15) *Coccinella 7-punctata*, L., s. ; (16) *C. 14-punctata*, L., s. ; (e) *Nitidulidæ* : (17) *Meligethes*, ab. C. Hymenoptera—(a) *Tenthredinidæ* : (18) *Athalia rosæ*, L. ; (19) Species of *Tenthredo* ; (b) *Ichneumonidæ* : (20) Various species ; (c) *Evaniidæ* : (21) *Fœnus affectator*, F. ; (d) *Sphegidæ* : (22) *Crabro lapidarius*, Pz. ♂ ♀ (Thur.), ab. ; (23) *Philanthus triangulum*, F. ; (e) *Vespidæ* : (24) *Odynerus sinuatus*, F. ♀ ; (25) *O. debilitatus*, Sauss. ; (26) *Vespa rufa*, L. ♀, s. ; (f) *Apidæ* : (27) Species of *Prosopis*, s. ; (28) *Andrena pilipes*, F. ♀, s. D. Lepidoptera—(29) *Argynnis Paphia*, L. (Willebadessen) (s. ?) E. Neuroptera—(30) *Panorpa communis*, L., l.h. See also No. 590, 1., and No. 609.

191. *PEUCEDANUM CERVARIA*, Lap.—On the slope of the Rehmburg, near Mühlberg in Thuringia, a locality rich in rare plants, I found on the last sunny days in August, 1869, the following insects, many of them rare, upon this still rarer Umbellifer :—

A. Diptera—(a) *Bombylidæ* : (1) *Anthrax maura*, L. ; (b) *Muscidæ* : (2) *Phasia crassipennis*, F., ab. ; (3) *Ph. analis*, F., scarce ; (4) *Gymnosoma rotundata*, L., very ab. B. Coleoptera—(a) *Chrysomelidæ* : (5) *Clythra scopulina*, L. ; (b) *Cerambycidæ* : (6) *Strangalia bifasciata*, Müller. C. Hymenoptera—(a) *Chrysidæ* : (7) *Hedychrum lucidulum*, F. ♂ ♀ ; (b) *Sphegidæ* : (8) *Crabro vagus*, L. ♀ ; (9) *Cr. cribrarius*, L. ♂ ♀, ab. ; (10) *Nysson macnatus*, v. d. L. ♀ ; (11) *Tachytes unicolor*, Pz. ♀ ; (12) *T. pectinipes*, v. d. L.

♀; (13) *Ammophila sabulosa*, L.; (14) *Psammophila viatica*, L. ♂; (15) *Pompilus viaticus*, L. ♂; (16) *Priocnemis bipunctatus*, F. ♀; (17) *Pr. obtusiventris*, Schiödte, ♀; (18) *Ceropales maculata*, F. ♀; (19) *C. variegata*, F. ♀ ♂; (20) *Tiphia femorata*, F., very ab., all licking honey; (c) *Vespidæ*: (28) *Polistes gallica*, L., and var. *diadema*; (d) *Apidæ*: (22) *Prosopis variegata*, F., s.; (23) *Halictus leucozonius*, Schrk. ♂ ♀, s. and c.p.; (24) *H. quadricinctus*, F. ♀, s.; (25) *Andrena minutula*, K. ♀, freq., c.p.; (26) *Megachile lagopoda*, Pz. ♀, once, sucking.

It is a remarkable fact that this scarce Umbellifer is visited by a choice collection of rare insects, while the most common visitants are absent. I do not think that this is due to a special taste of its honey, but I suppose that the same conditions necessary for the plant's existence are also favourable to special insects.

192. PEUCEDANUM (ANETHUM) GRAVEOLENS, L.—The dirty-yellow flowers of this plant are, like those of *Bupleurum*, visited by Diptera and Hymenoptera, but far more plentifully and by a greater variety of forms, owing, doubtless, to the strong odour of the flowers. No species of beetle occurs among the very numerous visitors.

Visitors: A. Diptera—(a) *Stratiomyidæ*: (1) *Chrysomya formosa*, Scop., s.; (b) *Bombylidæ*: (2) *Anthrax maura*, L. (Thur.); (c) *Syrphidæ*: (3) *Cheilosia scutellata*, Fallen; (4) *Syrphus pyrastris*, L., sucking, as also were the following: (5) *Eristalis arbustorum*, L.; (6) *E. nemorum*, L.; (7) *E. sepulcralis*, L.; (8) *E. tenax*, L.; (9) *Syrphia pipiens*, L.; (d) *Muscidæ*: (10) *Gymnosoma rotundata*, L., ab.; (11) *Lucilia cornicina*, F.; (12) *Musca corvina*, F.; (13) *Cyrtoneura simplex*, Loew., and *curvipes*, Macq., the last two identified by Herr Winnertz; (14) *Sepsis*, ab.; (e) *Tipulidæ*: (15) *Tipula* sp. B. Hymenoptera: (a) *Tenthredinidæ*: (16) Several species of *Tenthredo*; (b) *Ichneumonidæ*: (17) Numerous species; (c) *Evaniadæ*: (18) *Fœnus affectator*, F.; (19) *F. jaculator*, F. (Thur.); (d) *Formicidæ*: freq.; (e) *Chrysidæ*: (20) *Hedychrum lucidulum*, F. ♀ ♂, freq.; (21) *Chrysis ignita*, L. ♀; (22) *Chr. bidentata*, L. ♀; (f) *Sphegidæ*: (23) *Crabro sexcinctus*, v. d. L. ♂ (Thur.); (24) *Cr. vexillatus*, Pz. ♀ (Thur.); (25) *Cr. podagricus*, H. Sch. ♀ (Thur.); (26) *Cr. denticeris*, H. Sch.; (27) *Cr. Wesmæli*, v. d. L. ♂; (28) *Oxybelus uniglumis*, L., ab.; (29) *Tripoxylon clavicernum*, v. d. L. ♀; (30) *Cemonus unicolor*, F. ♀; (31) *Tacytes pectinipes*, L. ♀ (Thur.); (32) *Psen atratus*, Pz. ♀ ♂ (Thur.); (33) *Pompilus cinctellus*, v. d. L. ♀; (34) *P. neglectus*, Wesm. ♀ (Thur., July 14, 1870 !); (35) *Tiphia femorata*, F. ♂; (36) *Myrmosa melanocephala*, F. (Thur., July 14, 1870 !); (g) *Vespidæ*: (37) *Odynerus parietum*, L.; (38) *O. debilitatus*, Sauss.; (39) *Eumenes pomiformis*, L. ♂; (40) *Polistes gallica*, L. (Thur.); (h) *Apidæ*: (41) *Prosopis sinuata*, Schenck, ♂ ♀ (Thur.); (42) *Pr. communis*, Nyl. ♀ ♂ (Tekl. B.); (43) *Pr. armillata*, Nyl. ♂ (Tekl. B.); (44) *Sphecodes gibbus*, L. ♂ ♀, ab.; (45) *Andrena parvula*, K. ♀, c.p.; (46) *A. dorsata*, K. ♀, c.p.

## 193. PEUCEDANUM (PASTINACA) SATIVUM, L. (Thuringia):—

Visitors : A. Diptera—(a) *Bombylidae* : (1) *Anthrax flava*, Hffagg., l.h. ; (b) *Syrphidae* : (2) *Chrysotoxum bicinctum*, L. ; (3) *Syritta pipiens*, L. ; (c) *Muscidae* : (4) *Dexia rustica*, F. ; (5) *Onesia sepulcralis*, Mgn. ; (6) *Lucilia silvarum*, Mgn. ; (7) *Sarcophaga carnaria*, L. B. Hymenoptera—(a) *Tenthredinidae* : (8) Several species of *Tenthredo* ; (b) *Ichneumonidae* : (9) Numerous species ; (c) *Sphegidae* : (10) *Crabro sexcinctus*, v. d. L. ♂ ; (11) *Tiphia femorata*, F. ; (12) *Mutilla europæa*, L. ♀ ; (d) *Vespidae* : (13) *Polistes gallica*, L., and var. *diadema* ; (14) *Odynerus parietum*, L. ♂. See also No. 590, 1.

So the dull yellow flowers of this plant, like those of *Bupleurum* and *Anethum*, are visited only by Diptera and Hymenoptera, not by Beetles.

## 194. HERACLEUM SPHONDYLIIUM, L. :—

Visitors : A. Diptera—(a) *Bombylidae* : (1) *Anthrax flava*, Hff. (Sld. Tekl. B.) ; (b) *Empidæ* : (2) *Empis livida*, L. ; (c) *Asilidæ* : (3) *Dioctria Reinhardi*, Wied., ab. (Sld.) ; (d) *Syrphidæ* : (4) *Chrysotoxum bicinctum*, L. (Sld.) ; (5) *Ch. festivum*, L. (Tekl. B.) ; (6) *Pipizella virens*, F. ; (7) *P. annulata*, Macq. ; (8) *Chrysogaster viduata*, L. ; (9) *Cheilosia scutellata*, Fall. ; (10) *Syrphus glaucius*, L. ; (11) *S. ribesii*, L. ; (12) *S. pyrastris*, L. ; (13) *Melithreptus menthastri*, L. ; (14) *Ascia podagrica*, F. ; (15) *Eristalis tenax*, L. ; (16) *E. nemorum*, L. ; (17) *E. arbustorum*, L. ; (18) *E. sepulcralis*, L. ; (19) *E. æneus*, Scop. ; (20) *E. pertinax*, Scop. ; (21) *E. horticola*, Mgn. (Sld.) ; (22) *Helophilus florens*, L., ab. ; (23) *Xylota florum*, L. (Sld.) ; (24) *Syritta pipiens*, L. ; (e) *Conopidæ* : (25) *Zodion cinereum*, F. (Sld.) ; (f) *Muscidæ* : (26) *Echinomyia grossa*, L. (Haar) ; (27) *E. fera*, L. ; (28) *E. magnicornis*, Zett. ; (29) *Nemoræa* sp. ; (30) *Exorista vulgaris*, Fallen. ; (31) *Tachina erucarum*, Rond. ; (32) *Sarcophaga carnaria*, L., ab. ; (33) *S. hamarrhoa*, Mgn. ; (34) *Onesia sepulcralis*, Mgn. ; (35) *O. floralis*, Rob. Desv. ; (36) *Graphomyia maculata*, Scop. ; (37) *Lucilia sericata*, Mgn. ; (38) *L. Cæsar*, L. ; (39) *L. silvarum*, Mgn. ; (40) *L. cornicina*, F. ; (41) *Pyrellia ænea*, Zett. ; (42) *Musca corvina*, F. ; (43) *Calliphora vomitoria*, L. ; (44) *C. erythrocephala*, Mgn. ; (45) *Scatophaga merdaria*, F., ab. ; (46) *Sepsis cynipsea*, L., ab. ; (g) *Tabanidæ* : (47) *Tabanus rusticus*, L. ; (h) *Mycetophilidæ* : (48) *Platyura* sp. ; (i) *Tipulidæ* : (49) *Pachyrrhina histrio*, F. B. Coleoptera—(a) *Nitidulidæ* : (50) *Thalycra sericea*, Er. (Siebengebirge) ; (51) *Meligethes*, ab. ; (b) *Dermestidæ* : (52) *Anthrenus pimpinellæ*, F. ; (c) *Lamellicornia* : (53) *Hoplia philanthus*, Sulz., very freq. (Sld.) ; (54) *Trichodes fasciatus*, L., ab. ; (55) *Cetonia aurata*, L., very ab., (Sld. Siebengeb.) ; (d) *Elateridæ* : (56) *Agriotes ustulatus*, Schaller (Thur.) ; (57) *Corymbites holosericeus*, L. ; (58) *C. hæmatodes*, F. (Siebengeb., July 8, 1871) ; (e) *Malacodermata* : (59) *Telephorus melanurus*, F., very freq. ; (60) *T. fuscus*, L. ; (61) *T. lividus*, L. ; (62) *Trichodes apiarius*, L. ; (f) *Mordellidæ* : (63) *Mordella fasciata*, L. ; (g) *Edemeridæ* : (64) *Edemera virescens*, L. ; (h) *Cerambycidæ* : (65) *Rhagium inquisitor*, F. (Sld.) ; (66) *Pachyta 8-maculata*, F., ab. (Sld. Siebengeb.) ; (67) *Strangalia melanura*, L., very ab. (Sld.) ; (68) *S. nigra*, L. ; (i) *Chrysomelidæ* : (69) *Cryptocephalus sericeus*, L. ; (k) *Coccinellidæ* : (70) *Exochomus auritus*,

Scriba. C. Hymenoptera—(a) *Tenthredinidæ*: (71) *Tenthredo bifasciata*, L., ab.; (72) *T. notha*, Kl., not rare; (73) *T. tricineta*, F.; (74) *T. sp.*; (75) *T. annulata*, F.; (76) *Selandria serva*, F., very freq.; (77) *Athalia rosæ*, L.; (78) *Hylotoma rosarum*, F.; (79) *H. cærulescens*, F.; (80) *H. ustulata*, L.; (81) *H. vulgaris*, Kl.; (82) *H. femoralis*, Kl.; (83) *Cimbex sericea*, L., not rare (Sld.); (b) *Ichneumonidæ*: (84) Numerous species; (c) *Sphegidæ*: (85) *Crabro lapidarius*, Pz. ♀ ♂, freq.; (86) *Cr. vagus*, L. ♀ ♂; (87) *Cr. cribrarius*, L. ♀ ♂; (88) *Oxybelus uniglumis*, L., ab.; (89) *Philanthus triangulum*, F. ♀; (90) *Gorytes campestris*, L. ♀ ♂, not rare; (91) *Dinetus pictus*, F. ♀ ♂, ab.; (92) *Mimesa bicolor*, Sh. (Thur.); (93) *M. unicolor*, v. d. L. (Thur.); (94) *Pompilus viaticus*, L. ♂; (95) *P. pectinipes*, v. d. L. ♂; (96) *Priocnemis exaltatus*, F. (Thur.); (97) *Ceropales maculata*, F., not rare; (98) *Tiphia femorata*, F., ab.; (d) *Vespidae*: (99) *Odynerus parietum*, L., ab.; (100) *O. sinuatus*, F.; (101) *O. trifasciatus*, F. ♀; (102) *Vespa rufa*, L. ♀; (103) *V. holsatica*, F. ♂; (104) *V. vulgaris*, L. ♀; (e) *Apidae*: (105) *Prosopis armillata*, Nyl. ♀; (106) *Halictus cylindricus*, F. ♀, covered with pollen on the whole hairy ventral surface; (107) *H. leucopus*, K. ♂; (108) *H. flavipes*, F. ♀; (109) *Andrena nana*, K. ♀, s.; (110) *A. fucata*, Sm. ♀, ab., s. and c.p.; (111) *A. coitana*, K. ♀, not rare (Sld.); (112) *A. Rosæ*, Pz. ♀, freq.; (113) *Sphecodes gibbus*, L. ♂, s.; (114) *Nomada ferruginata*, K. ♀, s.; (115) *Megachile centuncularis*, L. ♀, c.p.; (116) *Bombus terrestris*, L. ♀, c.p.; (117) *Apis mellifica*, ♀, s. and c.p. D. Hemiptera—(118) Several bugs. See also No. 590, I., and No. 609.

### 195. DAUCUS CAROTA, L.:—

Visitors: A. Diptera—(a) *Stratiomyidæ*: (1) *Stratiomys Chamæleon*, Deg., ab.; (2) *S. riparia*, Mgn., ab.; (b) *Bombylidæ*: (3) *Anthrax flava*, Hff. (Thur.); (c) *Syrphidæ*: (4) *Pipizella annulata*, Macq.; (5) *Pipiza funebris*, F.; (6) *Chrysogaster viduata*, L.; (7) *Cheilosia soror*, Zett.; (8) *Syrphus pyrastris*, L.; (9) *Melithreptus scriptus*, L.; (10) *M. tæniatus*, Mgn.; (11) *Ascia podagrica*, F.; (12) *Eristalis sepulcralis*, L.; (13) *E. arbustorum*, L.; (14) *Helophilus floreus*, L.; (15) *Syritta pipiens*, L.; (d) *Muscidæ*: (16) *Gymnosoma rotundata*, L.; (17) *Sarcophaga albiceps*, Mgn. (Thur.); (18) Species of *Lucilia*; (19) Species of *Sepsis*. B. Coleoptera—(a) *Dermostidæ*: (20) *Anthrenus pimplinellæ*, F.; (b) *Lamellicornia*: (21) *Trichius fasciatus*, L.; (c) *Elateridæ*: (22) *Agriotes sputator*, L. (Thur.); (23) *A. ustulatus*, Schaller (Thur.); (24) *A. gallicus*, Lap. (Thur.); (d) *Malacodermata*: (25) *Dasytes pallipes*, Pz. (Thur.); (e) *Mordellidæ*: (26) *Mordella fasciata*, F.; (27) *M. aculeata*, L.; (f) *Curculionidæ*: (28) *Spermophagus cardui*, Sch. (Thur.); (g) *Cerambycidæ*: (29) *Strangalia bifasciata*, Müller (Thur.). C. Hymenoptera—(a) *Tenthredinidæ*: (30) *Hylotoma ustulata*, L. (Thur.); (31) *H. femoralis*, Kl. (Thur.); (32) *Selandria serva*, F.; (33) *Athalia rosæ*, L.; (34) *Tenthredo notha*, Kl.; (b) *Ichneumonidæ*: (35) Various; (c) *Chrysidæ*: (36) *Hedychrum lucidulum*, F. ♂ ♀ (Thur.), ab.; (d) *Sphegidæ*: (37) *Oxybelus uniglumis*, L., ab.; (38) *O. bipunctatus*, Ol.; (39) *Pompilus niger*, F. ♂; (40) *P. viaticus*, L. ♂; (41) *P. neglectus*, Wesm. ♂; (42) *P. intermedius*, Schenck; (43) *Priocnemis obtusiventris*, Schi. (Thur.); (44) *Ceropales maculata*, F.; (45) *Tiphia femorata*, F., freq.; (46) *Mutilla europæa*, L. ♂ (Thur., July 14, 1870); (47) *Cerceris variabilis*, Schr. ♀; (e) *Vespidae*: (48) *Odynerus sinuatus*, F. ♀;

(f) *Apidæ* : (49) *Prosopis variegata*, F. ♂ (Thur.) ; (50) *P. sinuata*, Schenck, ♂ ; (51) *Sphcodes gibbus*, L. ♀ ; (52) *Halictus albipes*, F. ♂ ; (53) *H. interruptus*, Pz. ♀ (Thur.) ; (54) *H. fulvicornis*, K. ♂ ; (55) *Andrena parvula*, K. ; (56) *A. nana*, K. ♀, s. ; (57) *Nomada lateralis*, Pz. ♀ (Thur.). D. *Lepidoptera*—(a) *Rhopalocera* : (58) *Hesperia lineola*, O., s. ; (b) *Tineina* : (59) *Nemotois*, Hbn., sp., s. E. *Hemiptera*—(60) *Tetyra nigrolineata*, L. (Thur.), ab. F. *Neuroptera*—(61) *Hemerobius*. See also No. 590, 1.

*Daucus (Orlaya) grandiflora*, Hoffm.—This species has three different kinds of flowers, all differing in form and degree of conspicuousness : (1) In the centre of the umbellule the florets are male only, and have small incurved petals ; (2) at the edge of the umbellule the florets are asexual, and the outermost petal is greatly enlarged ; (3) at the margin of the whole umbel are female florets, in which the outer petals attain a gigantic size (590, 1.).

*Caucalis daucoides*, L., is visited by *Tetyra nigrolineata*, L. (Hemiptera) (590, 1.).

#### 196. CAUCALIS (TORILIS) ANTHRISCUS, L. :—

Visitors : A. *Diptera*—(1) *Gymnosoma rotundata*, L., freq. B. *Hymenoptera*—(a) *Tenthredinidæ* : (2) *Tenthredo notha*, Kl. (Tekl. B.) ; (b) *Sphigidæ* : (3) *Crabro vagus*, L. ♀ ; (4) *Oxybelus bellicosus*, Ol. ; (5) *O. uniglumis*, L., ab. ; (6) *Ceropales maculata*, F. ♂ ♀, ab. ; (c) *Vespidæ* : (7) *Odynerus parietum*, L. ; (d) *Apidæ* : (8) *Prosopis variegata*, F. ♂. C. *Lepidoptera*—(9) *Pieris rapæ*, L. See also No. 590, 1.<sup>1</sup>

#### REVIEW OF THE UMBELLIFERÆ.

A survey of the Umbelliferæ and their insect-guests proves most definitely that in flowers otherwise constituted alike the visitors vary in abundance and variety in proportion to the conspicuousness of the flowers. For our comparison we must naturally choose flowers that have been observed to much the same extent. If we select a number, e.g. *Ægopodium*, *Carum*, *Pimpinella Saxifraga*, *Heracleum*, *Torilis*, *Anthriscus silvestris*, *Daucus*, and *Chærophyllum temulum*, and arrange them in the order of conspicuousness, this arrangement will not differ materially from the following, in which they are placed according to the number of

<sup>1</sup> The following additional species are discussed in my *Alpenblumen*.—*Bupleurum stellatum*, L. ; *Chærophyllum Villarsii*, Koch. ; *Gaya simplex*, Gaud. ; *Loserpitium hirsutum*, Lam. ; *Meum Mutellina*, Gärtn. ; *Peucedanum Ostruthium*, L. Lists of visitors to the following are given in my *Weitere Beobachtungen*, pt. 1. ; *Æthusa Cynopium*, L. ; *Bupleurum rotundifolium*, L. ; *Thyselinum palustre*, Hoffm.

different species of their insect-guests: 1. *Heracleum* (118); 2. *Ægopodium* (104); 3. *Anthriscus silvestris* (73); 4. *Daucus Carota* (61); 4. *Carum carui* (55); 6. *Chærophyllum temulum* (23) and *Pimpinella Saxifraga* (23); 7. *Torilis* (9).

Those insects which are most specialised for obtaining honey are the least frequent visitors of Umbelliferae. On most Umbellifers butterflies are never seen, and on the others only rarely. In cases where I saw them on several flowers one after another sinking their proboscides on to the fleshy disk, I have set them down as sucking; but the point may be reserved whether they really can suck up honey off the flat surface, or were tearing the disk with the sharp appendages of the proboscis and sucking the juice set free, or whether they were only looking for honey unsuccessfully.

We find on Umbellifers, on the one hand, the least specialised genera of bees (*Prosopis*, *Sphecodes*, *Halictus*, *Andrena*) licking the flat layer of honey or gathering pollen, and, on the other hand, the most diligent forms (*Apis*, *Bombus*.) collecting pollen, or more rarely sucking honey.

The odour of Umbellifers is shown to be of marked influence on bees' visits, as the strong-smelling umbels of *Anethum graveolens* are visited with special preference by the equally strong-smelling species of *Prosopis*. The great majority of the visitors of Umbellifers are short-lipped flies, beetles, wasps, and other short-lipped insects in immense variety. As a peculiarity which influences this assemblage of insects, I must mention the yellowish colour, for I have never found the flowers of *Bupleurum*, *Silaus*, or *Pastinaca* visited by beetles. These seem to be mainly attracted to flowers by bright colours.

Rare Umbellifers, confined to particular localities, have rare insects as their visitors.

#### ORD. ARALIACEÆ.

*Hedera*, L., is proteranderous, according to Delpino, and is fertilised by flies (177). I have seen it visited also by beetles and by wasps (590, 1.).

#### ORD. CORNACEÆ.

197. *CORNUS SANGUINEA*, L.—The fleshy ring surrounding the base of the style secretes honey, which, lying open on the flat

surface, is much more easily licked up by the tongues of short-lipped insects, or by the end-flaps (*labellæ*) of *Diptera*, than by the long proboscis of bees. I have never seen bees upon the flowers of *C. sanguinea*, although they may occasionally frequent them for the sake of pollen or even honey; but I have noticed many other insects licking the honey on these flowers.

Since the anthers are developed at the same time as the stigma, and since they open inwards and stand on a level with it at a little distance, the insect, alighting on the flower and bending its head down to the fleshy disk, generally touches the stigma with one side of its head or body and one or two anthers with the other; and so passing from flower to flower, and touching the stigma now with one side of its head now with the other,

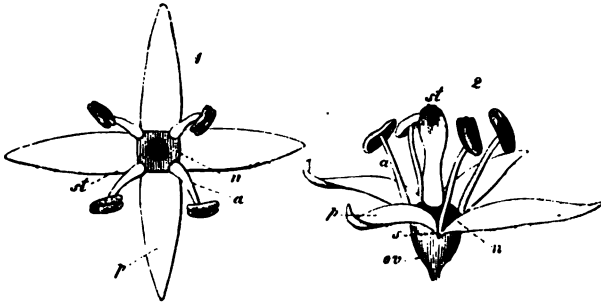


FIG. 95.—*Cornus sanguinea*, L.

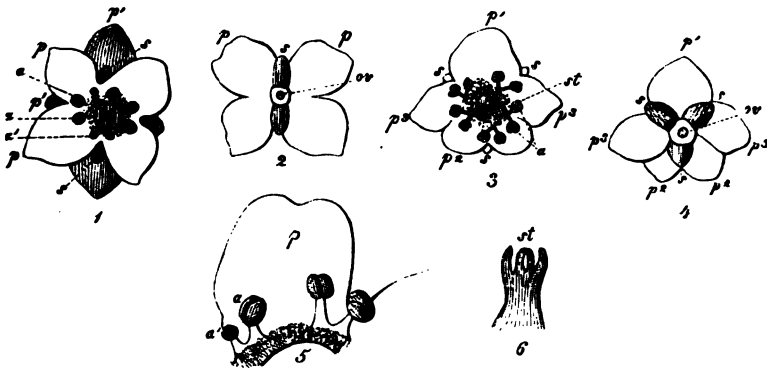
- 1.—Flower, from above.  
2.—Ditto, in side view.

it produces cross-fertilisation, especially as in its movements it touches anthers and stigmas with its legs or the underside of its body. Only the smaller insects (*Nitidulidæ*, *Byturus*, small *Diptera*) which creep about irregularly in the flowers can occasion self-fertilisation also. In default of insect-visits, pollination, and even cross-pollination, may here and there occur by the stigma accidentally touching an anther of a neighbouring flower.

Visitors : A. *Coleoptera*—(a) *Nitidulidæ* : (1) *Thalycra sericea*, Er.; (2) *Meligethes* ; (b) *Dermestidæ* : (3) *Byturus fumatus*, F.; (c) *Elateridæ* : (4) *Dolopius marginatus*, L. ; (5) *Athous niger*, L. ; (d) *Curculionidæ* : (6) *Otiorhynchus picipes*, F. ; (e) *Cerambycidæ* : (7) *Strangalia atra*, F. ; (8) *Str. armata*, Hbst. ; (9) *Str. attenuata*, L. ; (10) *Grammoptera lurida*, F. ; (11) *Gr. lævis*, F. ; (f) *Malacodermata* : (12) *Telephorus pellucidus*, F. B. *Diptera*—(a) *Empidæ* : (13) *Empis livida*, L. ; (b) (14) a small midge in very great numbers. C. *Hymenoptera*—*Sphagidæ* : (15) *Pompilus* sp. ; all the visitors were licking honey on the fleshy disk. See also No. 590, II.

## ORD. CAPRIFOLIACEÆ.

198. *ADOXA MOSCHATELLINA*, L.—The flat, exposed layer of honey limits or prevents the visits of long-tongued insects, while the greenish-yellow colour of the flowers must cause them to remain unnoticed by most flower-haunting Coleoptera. As in other flowers of a similar colour and displaying their honey in a similar way, the visitors are exclusively or almost exclusively Diptera and Hymenoptera, which in this case are specially attracted by the musky smell. The honey is secreted by a fleshy ring surrounding the bases of the stamens. The stamens

FIG. 96.—*Adoxa Moschatellina*, L.

- 1.—Apical flower, from above ( $\times 3\frac{1}{2}$ ).
  - 2.—Ditto, from below.
  - 3.—Lateral flower, not yet mature, unfolded artificially; the style is still bent down; viewed from the front.
  - 4.—Ditto, from behind.
  - 5.—Lobe of the corolla, with two (divided) stamens ( $\times 7$ ).
  - 6.—Stigma of the apical flower, from the side ( $\times 7$ ).
- a*, anther, not yet dehiscent; *a'*, ditto, after dehiscence; *s*, sepal; *p*, petals of the apical flower; *p'*, superior, *p''*, inferior, *p<sup>3</sup>*, lateral, petals of a lateral flower; *st*, stigma; *ov*, ovary; *n*, nectary.

are each split into two halves, and their pollen-covered surfaces are directed upwards in the terminal flowers, and outwards in the lateral flowers. Insects crawling over the small inflorescence bring their feet and proboscides in contact now with anthers now with stigma, and effect cross-fertilisation as in the case of the Guelder-rose and Elder (cf. Ricca, No. 665).

After my M.S. was finished I found a patch of *Adoxa* visited rather abundantly by small insects one sunny afternoon (April 7, 1872). I caught fifty-two examples of the following species. A. Diptera—(a) *Muscida*: (1) *Borborus niger*, Mgn., 2 specimens; (b) *Mycetophilida*: (2) various species

1½—4 mm. long., 11 specimens; (c) *Simulidæ*: (3) *Simulia* sp., 14 specimens; (d) *Cecidomyidæ*: (4) various species, 10 specimens. B. Hymenoptera—(a) *Pteromalini*: (5) *Eulophus*, ♂, 1 specimen; (6) seven other species, 9 specimens; (b) *Ichneumonidæ*: (7) *Pezomachus*, Grav., two species, 2 specimens. C. Coleoptera—*Curculionidæ*: (8) *Apion columbinum*, Grm., 3 specimens. Many of these small guests scrambled over the inflorescence, others flew from flower to flower; all licked the thin layer of honey, and none were feeding on the pollen.

199. *SAMBUCUS NIGRA*, L.—I have never found honey in the flowers. The relative positions of the essential organs are as in the following species, save that the stamens diverge still more widely. Many flowers are aggregated together, and the corymb is here so large and conspicuous that enlargement of the marginal flowers is unnecessary. The flowers are much less visited by insects than those of the Guelder-rose, and I have never found pollen-collecting bees upon them. It would be premature to



FIG. 97.—*Sambucus nigra*, L.

- 1.—Flower, from the front.
- 2.—Ditto, obliquely from the front and side.
- 3.—Ditto, obliquely from behind. ( $\times \frac{3}{4}$ )

conclude from this that the strong scent of the flowers is distasteful to bees, for I have frequently found bees, and even the hive-bee, visiting *Ruta graveolens*, in regard to which Delpino advanced the same opinion. Fertilisation is effected in the same way as in the previous species; but as cross-fertilisation is less perfectly insured, self-fertilisation takes place much more freely, pollen falling directly upon the stigma in many flowers.

Visitors: A. Diptera—(a) *Stratiomyidæ*: (1) *Sargus cuprarius*, L.; (b) *Syrphidæ*: (2) *Eristalis arbustorum*, L.; (3) *E. nemorum*, L.; (4) *E. tenax*, L.; (5) *E. horticola*, Mgn. (Sld.); (6) *Volucella pellucens*, L., all f.p. B. Coleoptera—*Lamellicornia*: (7) *Cetonia aurata*, L. (Sld.); (8) *Trichius fasciatus*, L., both of these beetles feed on the petals and other parts of the flower, and are therefore more destructive than useful. See also No. 590, III.

*Sambucus Ebulus*, L.—The flowers are visited on the Alps by hive-bees, humble-bees, and *Syrphidæ* (*Volucella*) (609, p. 392); in Low Germany by Diptera (590, III.).

200. *VIBURNUM OPULUS*, L.—The flowers are aggregated in a flat corymb, whose marginal flowers have the petals greatly enlarged at the expense of the essential organs. They thus attain conspicuousness, useless to themselves, but of the highest importance to the community, as Sprengel correctly explained (702, p. 159). When the flowers expand (Fig. 98, 2) the anthers have already begun to dehisce, and the stigmas are already so far developed that if pollen be applied to them it adheres easily and in large amount. Shortly afterwards the anthers become covered all round with pollen, and protrude, diverging, from the flower, while the stigmas remain in the base of the flower close above the ovary, whose upper surface secretes honey. The honey is fully exposed, and forms a flat, adherent layer, so that it is only attractive to flies and other

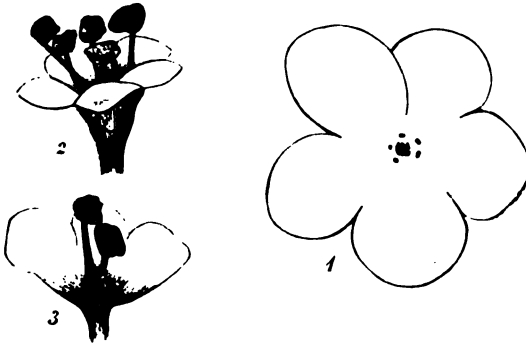


FIG. 98.—*Viburnum Opulus*, L.

- 1.—Marginal flower, from above, showing rudimentary pistil and stamens ( $\times 2\frac{1}{2}$ ).
- 2.—Fertile flower, soon after expansion ( $\times 4\frac{1}{2}$ ).
- 3.—Ditto, after removal of the anterior part of the corolla and stamens ( $\times 4\frac{1}{2}$ ).

short-lipped insects; the pollen attracts both flies and pollen-collecting bees; the white colour of the flowers makes them attractive to beetles, some of which are very destructive visitors. The most frequent visitors and the most efficient fertilisers are also those which get most benefit from the flowers, viz. flies, which by turns suck honey and feed on pollen. As each flower contains a very small amount of honey, the insects rapidly traverse the corymb; and they repeatedly effect fertilisation, which is usually cross-fertilisation, since in each flower anthers and stigmas generally come in contact with different parts of the insect's feet or proboscis. In absence of insects, self-fertilisation is not impossible, for, in spite of the divergence of the stamens, the stigma comes to lie in many flowers immediately below an anther.

Visitors: A. Diptera—(a) *Syrphidæ*: (1) *Eristalis arbustorum*, L.; (2) *E. nemorum*, L.; (3) *E. sepulcralis*, L.; (4) *E. tenax*, L.; (5) *Helophilus florens*, L.; (6) *H. pendulus*, L., all ab., s. and f.p.; (b) *Muscidæ*: (7) *Echinomyia fera*, L. B. Hymenoptera—*Apidæ*: (8) *Halictus sexnotatus*, K., c.p. C. Coleoptera—(a) *Nitidulidæ*: (9) *Meligethes*, ab.; (b) *Lamellicornia*: (10) *Phyllopertha horticola*, L., feeding on the petals and other parts of the flower. See also No. 590, III.

201. *SYMPHORICARPOS RACEMOSUS*, Michx.—The flowers of the Snowberry seem to be specially adapted for wasps, like those of *Scrophularia*. The corolla is pendulous, bell-shaped, and of a reddish colour, 7 to 8 mm. long and 5 mm. wide, cleft nearly to the middle into five lobes. A wasp's head (5 mm. broad, 2 to 2½ mm. thick) can be conveniently accommodated in it, and in point of fact, wasps, in places where they are abundant, are the most numerous visitors of this plant. The



FIG. 99.—*Symphoricarpos racemosus*, Michx. (2½.)

1.—Flower, viewed from the side.  
2.—Ditto, in section.

wasp hangs below the flower, thrusting in its head and licking the honey which is secreted very abundantly by the fleshy swelling at the base of the style. The honey collects in the base of the flower and on the inner wall of its dilated lower portion; it is prevented from flowing out by long close hairs upon the five lobes of the corolla extending inwards to the centre of the flower, and protected from

rain both by these hairs and by the obliquely pendulous position of the flower.

In the lowest part of the hairy lining, viz. that nearest the mouth of the flower, are the five anthers, which dehisce introrsely and converge towards the centre of the flower; the filaments are attached to the corolla near its middle. Immediately above the hairs, in the middle of the flower, stands the stigma, which ripens at the same time as the anthers. As the wasp thrusts its head wholly into the flower, it comes at once in contact with all five anthers and then touches with one side the stigma; but on its way to the stigma little or no pollen remains attached to it, partly because the pollen is very slightly adhesive, and partly because any grains that do attach themselves are brushed off before they reach the stigma by the hairs lining the corolla. It is only when being withdrawn moistened with honey that the insect's head acquires a plentiful coating of pollen to be carried to the stigma of the next flower. Thus, in case of wasps' visits, cross-fertilisation is insured;

in absence of insects, self-fertilisation cannot well occur owing to the relative positions of anthers and stigma.

Visitors: Hymenoptera—(a) *Vespidæ*: (1) *Vespa holsatica*, F.; (2) *V. media*, Degeer; (3) *V. saxonica*, F.; (4) *V. rufa*, L.; (5) *Polistes gallica*, L. and var. *diadema*; in Thuringia these five species make nine-tenths of all the visitors; in Lippstadt, where wasps are much less abundant and *Polistes* does not occur, the honey-bee preponderates; (6) *Odynerus* sp., bit holes in the corolla and introduced its head; (b) *Apidæ*: (7) *Apis mellifica*, L. ♀, ab.; (8) *Bombus agrorum*, F. ♀; (9) *B. pratorum*, L. ♀; (10) *B. muscorum*, F. ♀, all three species scarce; (11) *Eucera longicornis*, L. ♂; (12) *Megachile centuncularis*, K. ♂, all s.; (13) *Halictus sexnotatus*, K. ♀, s. and c.p.; (c) *Sphigidæ*: (14) *Ammophila sabulosa*, L., s. See also No. 590, III.

*Linnaea borealis*, Gron.—The position of the flower shelters the honey from rain, and hairs on the interior of the corolla exclude many small insects. Five purple lines on the interior of the corolla and a patch of orange colour on its inferior side, near the base, act as honey-guides. Cross-fertilisation is favoured by the position of the stigma in advance of the anthers (609, Fig. 158).

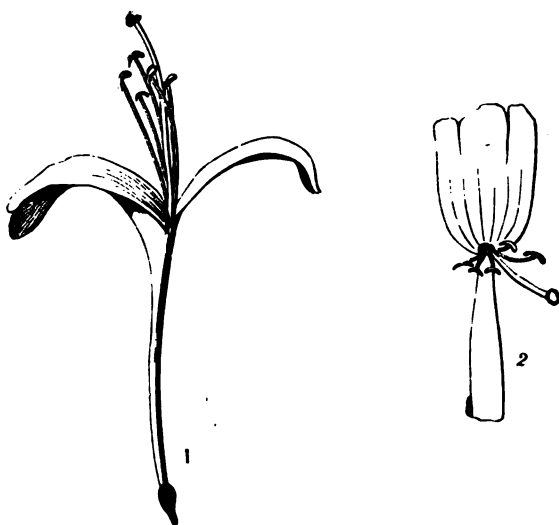


FIG. 100.—*Lonicera Caprifolium*, L.

1.—Flower, from the side. Nat. size. The figure should be horizontal.  
2.—Ditto, from the front.

202. *LONICERA CAPRIFOLIUM*, L.—The flowers are adapted for fertilisation exclusively by long-tongued crepuscular and nocturnal Lepidoptera. They bloom at the season when hawk-moths are

most abundant (May, June), they expand and exhale their perfume most strongly in the evening, and they conceal their honey in so long and narrow a tube that Lepidoptera alone of our native insects are able to reach it. The tube, whose inferior fleshy part secretes honey along its middle line, is about 30 mm. long, and for the greater part of its length only 1 to 2 mm. wide, and still further narrowed by the style; while the longest proboscides among our native bees measure 21 mm. (*Bombus hortorum* and *Anthophora pilipes*), and among our flies only 11 to 12 mm. (*Rhingia*, *Bombylius discolor*). Certainly the tube becomes filled to past the middle with honey so that even insects with a proboscis 15 mm. long can reach part of it; but this depth of honey is only attained in the evening, when bees and flies have ceased to seek their food. I have never seen bees or flies sucking on this honey-suckle; and it is all the more plentifully visited by hawk-moths on the warm, calm evenings of May and June. I caught on a single plant on May 27 and 29, 1868:—

Lepidoptera—(a) *Sphingidæ*: (1) *Sphinx convolvuli*, L. (65—80), 2 specimens; (2) *S. ligustri*, L. (37—42), 6 specimens; (3) *S. pinastri*, L. (28—33), 5 specimens; (4) *Deilephila elpenor*, L. (20—24), 17 specimens; (5) *D. porcellus*, L. (20), 1 specimen; (6), *Smerinthus tilia*, L. (23), 1 specimen; (b) *Noctuæ*: (7) *Dianthæcia capsicola*, S. V. (23—25), 2 specimens; (8) *Cucullia umbratica*, L. ♂ (18—22), 2 specimens; (9) *Plusia gamma*, L. (15), 1 specimen; (c) *Bombyces*: (10) *Dasychira pudibunda*, L. (0), 1 specimen.

*Smerinthus tilia* and *Dasychira pudibunda* which have completely aborted proboscides were doubtless attracted by the smell only, without having anything to gain from the plant; *Plusia gamma* might sip a little honey from untouched flowers, and the four preceding species might drink deeply, but only the first three could drain the honey. I examined the specimens I had collected not only with reference to the length of their tongues but also with reference to the extent to which they were dusted with pollen. In all (except the two last short-lipped species), at least the hairs upon the palps which cover the base of the proboscis were richly covered with pollen; and in several of the larger species the hairs and scales on the whole of the under side of the body from the head to the middle of the abdomen, including the proboscis, antennæ, legs, and wings, were thickly dusted. The most richly coated were individuals of the first three *Sphingidæ*, which had flown violently away, while *Dianthæcia*, *Cucullia*, and *Plusia* were the least so. The pollen-grains are rounded tetrahedra, .047 mm. in diameter; they adhere to the hairs and scales of the

insect and afterwards to the stigma by their sticky surface, and by the aid of small, sharp processes with which they are thickly covered.

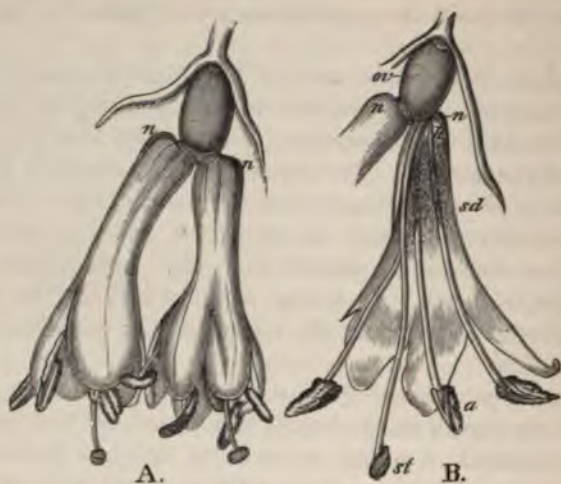
The visits of the above-named Lepidoptera result, in spite of the simultaneous development of anthers and stigma, regularly in cross-fertilisation, in consequence of the position of the stigma in advance of the anthers. The stamens project about 15 to 18 mm. and the style about 25 mm. beyond the mouth of the flower; both are slightly curved upwards at their ends, and the pollen-covered faces of the anthers are turned upwards. Lepidoptera, whether they alight, or suck the honey while poised in the air, must touch first the stigma and then the anthers with their ventral surfaces.

On warm, calm evenings, insect-visits are so abundant that on the following day all the flowers are found to have had their pollen entirely removed. On the other hand, on days following cool, windy evenings, the flowers display abundant pollen, which is then gathered by bees and flies.

On such days I have found the honey-bee and *Halictus sexnotatus*, K. ♀, busy collecting, and several Syrphidæ, *Xylota segnis*, L., *Rhingia rostrata*, L., and *Syrphus ochrostoma*, Zett., busy feeding on the pollen which remained upon the anthers. These secondary visitors occasionally effect fertilisation, but they must perform self-fertilisation as readily as cross-fertilisation, and at any rate the flower has not been adapted for them.

*Lonicera cærulea*, L.—The yellowish-white flowers are adapted for humble-bees, by which they are chiefly visited and fertilised. The tube is over 10 mm. long and pendulous. The stigma stands well in advance of the anthers, favouring cross-fertilisation; but in the absence of insects, pollen may easily fall on the stigma and effect self-fertilisation (609).

*Lonicera Periclymenum*, L.—The general structure of the flower resembles that of *L. Caprifolium*, and the plant is visited and fertilised by the same hawk-moths. The tube, however, is only 22 to 25 mm. long, so that the honey as soon as it has collected to the depth of a few millimetres is accessible to many of our bees. On July 17, 1867, I saw *Bombus hortorum*, L. ♀ (21 mm.), sucking honey from some flowers of *L. Periclymenum*. The bee wasted considerable time in obtaining a convenient position for sucking, and it crawled from the broad upper lip to the mouth of the tube without touching the stigma and anthers; and the amount of honey it obtained must have been small, for after visiting a few

FIG. 101.—*Lonicera caerulea*, L.A.—Pair of pendulous flowers ( $\times 3$ ).B.—Flower in section ( $\times 4$ ).

(Bergün, June 9, 1879.)

FIG. 102.—*Lonicera Periclymenum*, L.2.—A Hawk-moth (*Sphinx Ligustri*) sucking one of the flowers.

3.—Corolla, slit down the middle line superiorly, and laid open. n, nectary.

4.—Stigma.

5.—Section of ovary.

6.—Ovary and calyx.

flowers it flew away, though the plants were in full bloom. Bees, therefore, are only accidental visitors, which have had no influence in developing the special characters of the flower.<sup>1</sup>

203. *LONICERA TATARICA*, L.—Honey is secreted and lodged in the shallow pouch at the base of the tube, which is 6 to 7 mm. long. Stigma and anthers are matured simultaneously, and protrude from the flower in close proximity with one another, the stigma being slightly overtopped by the anthers. An insect-visitor inserts its head between the anthers and stigma, and so dusts one side with pollen while the other comes in contact with the stigma. The flowers stand unsymmetrically in pairs, causing the insect's head to enter in various positions and so favouring cross-fertilisation. When the stigma is thrust aside, its opposite side usually comes in contact with those anthers which are not touched by the insect's head, and it thus becomes dusted simultaneously with the pollen of its own flower. Flowers are frequently found in which the stigma is in close contact with one or two anthers, and self-fertilisation doubtless often takes place in absence of insects.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♂, s., ab.; (2) *Megachile centuncularis*, L. ♂, s.; (3) *Andrena albicans*, K. ♀, tries in vain to reach the honey. B. Diptera—*Syrphidae*: (4) *Rhingia rostrata*, L., s. and f.p., very ab.

*Lonicera nigra*, L.—This species is adapted for bees, which alight not on the under lip, which is bent backwards out of the way, but on the style and stamens. The flowers are homogamous. The stigma stands below the anthers, and in absence of insects self-fertilisation must occur (609, Fig. 159).

204. *LONICERA XYLOSTEUM*, L.—Honey is secreted and lodged as in *L. tatarica*, but the tube is only 3 to 4 mm. long. The anthers and stigma are matured simultaneously and project far beyond the mouth of the flower; the former are divergent and stand at a distance from the stigma. Humble-bees thrust their heads sometimes to one side sometimes to the other, sometimes above sometimes below the anthers, and in the course of repeated visits they dust their heads (or head and thorax) all round with pollen. In each flower one side of the bee's head touches the stigma and the other the anthers, so that cross-fertilisation proceeds regularly. I have never found flowers in which the anthers stood in immediate

<sup>1</sup> See No. 590, III. p. 75, for a case of atavism in this species.

contact with the stigma; but in the absence of insects, self-fertilisation may result in many flowers by pollen falling upon the stigma.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, very ab., s.; (2) *Bombus muscorum*, F. ♀, s.; (3) *B. pratorum*, L. ♀, s. B. Diptera—(a) *Empidae*: (4) *Empis opaca*, F., s., ab.; (b) *Syrphidae*: (5) *Rhingia rostrata*, L., s. and f.p.

The chief fertilisers are humble-bees, since they never insert their tongues into a flower without touching stigma and anthers with opposite sides of the head; while flies and the honey-bee never touch the stigma at all in many flowers.

*Lonicera alpigena*, L.—This species is fertilised by bees and humble-bees, and also still more frequently by wasps. It resembles



FIG. 103.—*Lonicera alpigena*, L.

A pair of recently expanded flowers ( $\times 4$ ). The flower on the right hand has an additional stamen. (Bergün, June 8, 1879.)

other wasp-fertilised flowers (*Scrophularia*, *Symphoricarpos*, *Epipactis palustris*) in having an expanded pouch-like honey-receptacle containing an unusually large supply of honey, and it is just wide enough to admit a wasp's head easily. The flower is reddish-brown in colour, like that of *Scrophularia* (609).

*Weigelia (Diervilla) rosea*, L.—The flower is adapted for bees, and undergoes a change of colour after fertilisation like *Ribes aureum* (590, III.).

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#### REVIEW OF THE CAPRIFOLIACEÆ.

The small group of *Caprifoliaceæ* is remarkable for the great variety of visitors to which nearly related plants have adapted themselves, chiefly by differences in the length of the tube. *Lonicera Caprifolium*, L., with a tube about 30 mm. long, permits only a few Lepidoptera to reach the honey; *L. Periclymenum*, L., in which the tube is only 20 mm. long, admits also a few specially long-tongued bees; *L. cærulea*, L., with a pendulous corolla and a tube over 10 mm. long, is adapted for humble-bees; in *L. tatarica*, L., and *L. Xylosteum*, L., the length of the tube falls to 7 to 3 mm. and certain long-tongued flies, in addition to a larger company of bees, visit and fertilise the flowers; the short, wide honey-receptacles of *Symphoricarpos* and *Lonicera alpigena*, L., are easily accessible even to wasps, which are attracted in great numbers by the large supply of honey; *Linnaea* is furnished with an infundibuliform corolla, but apparently attracts, for the most part, flies; in *Viburnum* the honey is freely exposed, but only as a flat, adherent layer, and the plant is visited chiefly by short-lipped insects, *e.g.* flies and beetles; *Sambucus* attracts a similar set of insects, which are less varied and fewer in number owing to the absence of honey; *Adoxa* attracts only minute honey-seeking insects. In case of insect-visits, cross-fertilisation is insured in all, but in very various ways; self-fertilisation in the absence of insects is rendered possible in those species which are least visited. In the least specialised and most generally accessible *Caprifoliaceæ* (*Adoxa*, *Sambucus*, &c.) the flowers are white or greenish; in those species fertilised by wasps they are reddish (*Symphoricarpos*) or reddish-brown (*Lonicera alpigena*, L.); in several species of *Lonicera* fertilised by bees (*e.g.* *L. tatarica*) they are bright red, in *L. cærulea* they are yellowish-white, but they are pale in those species which have the longest tubes and are adapted for crepuscular Lepidoptera (*L. Periclymenum*, *L. Caprifolium*).

## ORD. RUBIACEÆ.

205. *GALIUM MOLLUGO*, L.—A fleshy disk lying upon the ovary and surrounding the base of the style secretes honey, but in such small amount that it remains adhering in a very thin layer to the disk. In young flowers (Fig. 104, 1) the anthers stand erect and are covered all round with pollen, while the two stigmas as yet lie close together. Afterwards the stamens spread out horizontally, and finally their ends curve downwards between the petals outside the flower, while at the same time the two styles diverge (Fig. 104, 2). The stigmatic papillæ seem to be as well developed in the first period as in the second, and are not unfrequently covered with pollen while the stigmas still stand close together. The movement

FIG. 104. — *Galium Mollugo*, L.

- 1.—Young flower, with stamens and styles erect.
  - 2.—Older ditto. The stamens are bent out of the flower, and the styles have separated.
  - 3.—Centre of the flower, from above, more magnified.
- a, two stigmas; b, fleshy disk above the ovary.

of the stamens seems therefore not to be accompanied by dichogamy, but to be the sole contrivance to prevent self-fertilisation and, in case of insect-visits, to insure cross-fertilisation.

The thin layer of honey can scarcely tempt long-tongued insects to repeated visits. The colour of the flowers,—yellowish-white in the bud and in the young flower, becoming purer white afterwards,—seems to repel all those insects, *e.g.* beetles, which are only attracted by bright colours. In this relation a comparison of the insect-visitors of *G. Mollugo* and *G. verum* is instructive.

In this and the following species of *Galium* the pollen is conveyed to the stigma chiefly by the feet and, in a less degree, by the probosces of insects creeping over the inflorescence.

Visitors : A. Diptera—(a) *Stratiomyidæ* : (1) *Odontomyia viridula*, F., l.h., not rare ; (b) *Bombylidæ* : (2) *Anthrax flava*, Hffs. (Thur.), do. ; (3) *Systæchus sulfureus*, Mik. (Thur., Sld.), s., probably boring into the nectary ; (c) *Syrphidæ* : (4) *Syritta pipiens*, L., ab., s. and f.p. ; (5) *Syrphus ribesii*, L., s.

and f.p., not rare; (*d*) *Muscidæ*: (6) *Musca corvina*, F.; (7) *Scatophaga merdaria*, F., s.; (*e*) *Tipulidæ*: (8) *Pachyrrhina crocata*, L., s. B. Hymenoptera—*Sphégidæ*: (9) *Ammophila sabulosa*, L. ♀, once only,—I could not see whether it gained anything from the flowers. See also No. 590, III.

*Galium silvestre*, Poll.—This species resembles *G. Mollugo* in the mechanism of its flower; it is frequented on the Alps by Syrphidæ and by numerous Lepidoptera (No. 609, Fig. 156).

206. *GALIUM VERUM*, L.—The structure of the flower agrees closely with that of *G. Mollugo*. Different individuals show a very marked difference in the size of their flowers (Fig. 105, 1—4); but since the flowers are rendered conspicuous merely by aggregation, a diminution in their size does not diminish the number of insect-visitors so seriously as it does in most cases. The apparently unimportant circumstance that the flowers are bright yellow, and

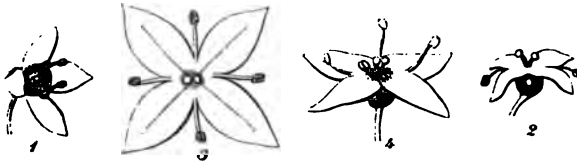


FIG. 105.—*Galium verum*, L.

- 1.—Young flower, of a small-flowered plant ( $\times 7$ ). The anthers are erect, and covered with pollen; the stigma is not yet mature.
- 2.—Older flower, of the same plant. The shrivelled anthers are bent out of the flower; the stigmas are mature and divergent.
- 3.—Flower, of a large-flowered plant; older than 1, but younger than 2 ( $\times 7$ ).
- 4.—Ditto, from the side.

not yellowish-white as in *G. Mollugo*, leads to the plant being visited by Coleoptera in addition to the other orders.

*G. verum* is very scarce near Lippstadt, and I have only watched its flowers once or twice in Thuringia and in Sauerland, so I have not obtained a long list of insect-visitors.

A. Diptera—(*a*) *Conopidæ*: (1) *Conops flavipes*, L. (Sld.); (*b*) *Muscidæ*: (2) *Ulidia erythrophthalma*, Mgn., ab., l.h. (Th.). B. Coleoptera—(*a*) *Lamellicornia*: (3) *Cetonia aurata*, L., ab. (Th.); (*b*) *Elatridæ*: (4) *Agriotes gallicus*, Lap. (Th.); (*c*) *Mordellidæ*: (5) *Mordella fasciata*, F. (Th.); (6) *M. aculeata*, L. (Th.). C. Hymenoptera—*Tenthredinidæ*: (7) *Tenthredo rapæ*, K. (Sld.). See also No. 590, III.

*Galium boreale*, L.—This species agrees with *G. silvestre* in regard to the position of its honey, its imperfect proterandry, the relative positions of stamens and pistil, and therefore also in the probability of cross-fertilisation in case of insect-visits, and the possibility of self-fertilisation in absence of insects (590, 609).

*Galium boreale*, L., *palustre*, L., and *uliginosum*, L., are all stated by Axell to be proterandrous (17).

*Galium tricornis*, With.—Honey is abundant, but the small isolated flowers are very inconspicuous and very little visited. They cannot dispense with the power of self-fertilisation, which takes place regularly, as the stamens do not curve outwards till they wither (590, III.).<sup>1</sup>

207. *ASPERULA CYNANCHICA*, L.—Honey is secreted, as in *Galium*, by a fleshy ring surrounding the base of the style, but it exists not as a smooth adherent layer but filling up the base of the tube; the latter is 2 mm. long. Anthers and stigmas mature simultaneously. The two stigmas stand close together in the middle of



FIG. 106.—*Asperula cynanchica*, L.

1.—Flower, with smooth white petals, from above ( $\times 7$ ).

2.—Ditto, after removal of half of the corolla.

3.—Ditto, with rough petals, marked with red lines.

4.—Ditto, from above.

ov, ovary; n, nectary; st, stigma; a, anther.

the tube; the anthers converge towards one another in the throat of the corolla. In case of insect-visits, cross-fertilisation is favoured by this condition only, that in consequence of the convergence of the anthers the proboscis of an insect-visitor is less readily dusted with pollen in entering a flower than in being drawn out, and also that the proboscis usually comes in contact with pollen on one side only and rubs the stigma with the opposite side (cf. *Myosotis*). In absence of insects, self-fertilisation occurs by part of the pollen falling on the stigma. On sunny slopes in Thuringia (Mühlberg, near Erfurt) I found this species bearing two different forms of flowers. Many plants had smooth, white, somewhat obtuse petals (Fig. 106,

<sup>1</sup> The following additional species of *Galium* are discussed in No. 590, III.: *G. saxatile*, L.; *G. silvaticum*, L.

1, 2); on other plants, the petals were rough on the upper surface, marked with a red elliptic line, and with another red line traversing the long axis of the ellipse, and were produced at the end into a slightly recurved point.

Visitors : A. Hymenoptera—*Apidæ* : (1) *Bombus muscorum*, F. ♀ (Thur., July 8, 1872), a. B. Diptera—*Bombylidæ* : (2) *Systæchus sulfureus*, Mik., a. (Thur., July 14, 1868). Additional visitors (four beetles, six flies, two Lepidoptera) are enumerated in No. 590, III.

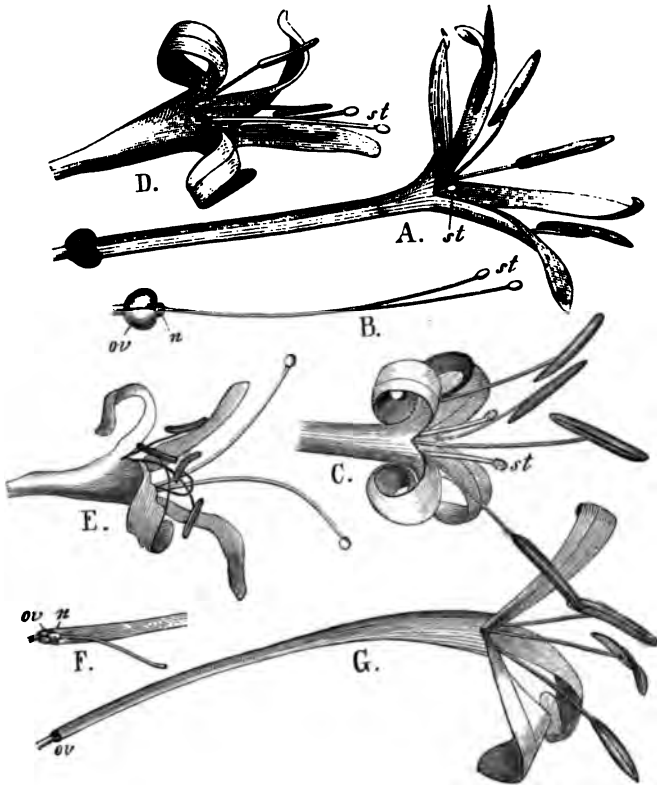


FIG. 107.—*Asperula taurina*, L.

- A.—Hermaphrodite flower, from the side.
- B.—Pistil of the same flower, with nectary.
- C.—Hermaphrodite flower, with the lobe of the corolla revolute, the stigmas more exserted, and their papillæ obvious.
- D.—A flower, whose stigmas overtop the black shrivelled anthers on which a few pollen-grains still lie.
- E.—Half-withered flower, in which the styles project still further.
- F.—Abortive pistil of a male flower.
- G.—Male flower, with three teeth, from the side. ( $\times 7$ )

(Churwalden, May 31, 1879.)

*Asperula taurina*, L.—This plant is adapted for nocturnal Lepidoptera by its white colour, and by its long, narrow tube,

9 to 11 mm. long. The plant is andromonœcious, and the hermaphrodite flowers are markedly proterandrous (609).

*Asperula azurea* is adapted for diurnal Lepidoptera (590, III).

*Asperula odorata*, L.—In the structure of the flower and the length of the tube this species closely resembles *A. cynanchica*. The hive-bee is a frequent visitor. Additional visitors (four beetles, four flies, one moth) are enumerated in No. 590, III.

*Sherardia arvensis*, L., is gynodiœcious (590, III, 605).

*Manettia*, Mut., is very diligently visited by humming-birds in South Brazil (360).

*Coffea arabica*, L., according to Bernouilli,<sup>1</sup> produces in Guatemala, at the beginning of the season, small pistillate fertile flowers. Prof. Ernst was unable to discover these small flowers at Caracas (224).

Brazilian species of *Borreria*, *Hedyotis*, and *Manettia* are dimorphic (Fritz Müller, 353); *Hedyotis* had already been shown to be dimorphic by Treviranus (742).

*Mitchella*, *Knoxia*, and *Cinchona* are dimorphic according to Darwin (154, 167).

*Chasalia*, *Nertera*, *Ophiorrhiza*, and *Luculia* are dimorphic according to Kuhn (399).

Other heterostyled Rubiaceæ are mentioned by Darwin in his *Forms of Flowers*, where he also discusses the passage from *heterostyly* to *diœcism* in this order.

*Faramca*, Aubl.—My brother Fritz Müller (554) gives an account of a dimorphic species of this genus, which is of interest in several respects. (1) It affords the only known instance of a striking difference in the character of the surface of the two kinds of pollen-grains. The smaller pollen-grains, which are produced in the long-styled flowers (whose anthers are inclosed in the tube), are smooth; the larger pollen-grains of the exerted anthers of the short-styled flowers are covered with short, rather close points, which prevent their being dispersed by a puff of wind. The pollen of the long-styled flowers, lying low down in the corolla, is in no danger of being blown away. (2) In the short-styled form the stamens twist round upon their axes, so as to turn their pollen-covered faces outwards. The short stamens (of the long-styled flowers) do not rotate but dehisce on their inner sides; and in both cases the pollen is thus placed in the best position for adhering to an insect's proboscis when inserted in the flower. But it is a very remarkable fact that this faculty of rotation is by no means

<sup>1</sup> *Bol. Zeitung*, 1869, p. 17.

perfect, for many of the long stamens do not twist properly, and to a great extent waste their pollen.

*Posoqueria (Martha) fragrans*, Roxb.,<sup>1</sup> has been described by my brother Fritz Müller (549).<sup>2</sup> It affords a most remarkable example of adaptation to Sphingidæ. The white colour of the flowers, their strong perfume, the long, narrow tube 11 to 14 cm. long, all point it out as such. The abundant honey at the base of the tube can only be reached by the tongues of Sphingidæ; and only these insects, e.g., *S. rustica*, L., whose proboscis is 15 mm. long, have been seen to visit the flower (F. Müller, Oct. 1873).

The five exerted anthers are united into an oval knob directed obliquely downwards and containing the loosely coherent pollen which escaped from the anthers before the expansion of the flower. The filament of the inferior stamen possesses a very great elastic tension acting upwards, those of the superior and lateral stamens have a similar tension outwards. The insect's proboscis has only one available point at which to enter the flower, and when in doing so it touches one of the superior stamens at a certain spot the tension of the filaments is released. The inferior stamen springs up with such violence that it hurls the loosely coherent pollen against the insect's proboscis at an angle of 50° with the tube of the corolla, and with an initial velocity of about 3 mm. per second; at the same time it closes the entrance of the tube. The superior and lateral stamens spring at the same time to the sides, the empty anthers of a superior and a lateral stamen remaining coherent on either side. About twelve hours afterwards the inferior stamen extends itself again and leaves the entrance to the honey open once more. If a hawk-moth, after exploding a flower in the male stage, comes to one in the stage under consideration, it is repaid for its startling reception in the former case by a rich supply of honey; and in thrusting its pollen-dusted proboscis down to the base of the flower it brings it in contact with the stigma which stands in the middle of the tube.

My brother, in his paper on *Fareamea* (554), refers again to *Posoqueria*, and points out that most of the flowers (whose only fertilisers are abroad in the evening) open towards evening, but that a considerable number open at various hours of the day, sometimes even in early morning, and that these are exploded by diurnal insects which cannot effect fertilisation. This is

<sup>1</sup> *Griffithia fragrans*, W. A.

<sup>2</sup> Darwin wrote to me: "Your brother's paper on *Martha* is, I think, one of the most wonderful ever written."

another interesting case of an adaptive modification imperfectly attained.

The Rubiaceæ include more dimorphic (heterostyled) genera than any other order. Darwin (167) discusses many of these cases, enumerating seventeen dimorphic genera, in addition to which *Chasalia*, Commers., *Ophiorrhiza*, L., and *Luculia*, Sweet, are mentioned by Kuhn (399). Darwin discusses the probable transition from heterostylism to dioecism in Rubiaceæ. *Mitchella*, L., which is normally heterostyled, is in some places dioecious (Meehan, 465). *Asperula scoparia*, Hook., and *A. pusilla*, Hook., two Tasmanian species, were stated by Treviranus (742) to be dimorphic, but according to Darwin the former at any rate is dioecious. Our own *Asperula taurina*, L., and *Galium cruciatum*, With., are both andromonœcious, and *Sherardia arvensis*, L., is gynodioecious (605).

#### ORD. VALERIANEÆ.

Delpino in his work on the Artemisiaceæ rightly insists that the calyx in Compositæ could only become transformed into a pappus after the involucreal bracts had assumed the usual functions of a calyx; and he considers the Valerianæ to be offshoots of the Compositæ, which have in part retained this hereditary development of a pappus, and in part have acquired other means of dissemination of the seeds by the wind.

208. VALERIANA OFFICINALIS, L.,<sup>1</sup> is distinctly proterandrous. The florets, in spite of their small size, are rendered conspicuous by aggregation. In each floret the tube is 4 to 5 mm. long, and half a millimetre from the base is a small pouch with a green, fleshy floor, which secretes and lodges the honey; this is accessible to numerous insects with moderately short proboscides, especially as the tube widens above to a diameter of 2 mm. Insect-visits are numerous and various, and the well-marked dichogamy ensures cross-fertilisation in case of insect-visits. In the first period the anthers, covered all round with pollen, in the second the three outspread stigmas, project freely from the flower, and are touched by the feet and under surfaces of insects creeping over the inflorescence and by the heads of insects sucking honey from the florets; in the second period the anthers are bent away outside the floret. I have never seen florets which fertilised themselves; stigmas which

<sup>1</sup> Compare Sprengel, No. 702, pp. 63-65.

come in contact with the anthers of neighbouring flowers are, on the other hand, not uncommon.

Visitors : A. Hymenoptera—*Apidae* : (1) *Apis mellifica*, L. ♀, ab. ; (2) *Bombus pratorum*, L. ♀, s. ; (3) a small *Halictus*, ♀ ♂, s. B. Diptera—(a) *Tabanidae* : (4) *Tabanus luridus*, Pz. ; (b) *Empidae* : (5) *Empis livida*, L. ; (6) *E. rustica*, F., both species very ab., s. ; (c) *Syrphidae* : (7) *Eristalis nemorum*, L. ; (8) *E. arbustorum*, L. ; (9) *E. sepulcralis*, L. ; (10) *E. horticola*, Mgn. (Sld.) ; all four species ab., f.p. ; (11) *Volucella bombylana*, L. ; (12) *Helophilus florens*, L. ; (13) *H. pendulus*, L. ; (14) *Syritta pipiens*, L. ; (15) *Chrysotoxum festivum*, L., all sometimes s., sometimes f.p. ; (d) *Conopidae* : (16) *Sicus ferrugineus*, L., s. ; (e) *Muscidae* : (17) *Sarcophaga carnaria*, L. ; (18) *Onesia floralis*, E. D. ; (19) *Lucilia cornicina*, F. ; (20) *Musca domestica*, L. ; (21) *Calliphora erythrocephala*, Mgn. ; (22) *C. vomitoria*, L., all ab., s. See also No. 590, III. I have found it visited on the Alps by one beetle, sixteen species of Coleoptera, and fifteen Lepidoptera (609).

209. *VALERIANA DIOICA*, L.<sup>1</sup>—Honey is secreted as in the previous species, but cross-fertilisation is ensured not by dichogamy, but by diœcism. The male flowers, being notably larger than the female, are almost always visited first by the insect, as I have repeatedly observed. Sprengel insisted rightly that in this order alone could the insect-visits be useful to the plant. In the male florets the tube is  $2\frac{1}{2}$  to  $3\frac{1}{2}$  mm. long, widening above ; in the female it is only 1 mm. long, so that in both the honey is accessible to insects with very short proboscides. The capitulum is much less conspicuous than in *V. officinalis*, but the flowering period is so early that the plant is exposed to much less competition. Insect-visitors are less various than in the previous case, but still fairly numerous. In this plant there are four kinds of individuals, with four different kinds of flowers : (1) male flowers without any rudiment of a pistil, and with large corollas ; (2) male flowers with a rudimentary pistil, and a somewhat smaller corolla ; (3) female flowers with evident traces of anthers, and with still smaller corollas ; (4) female flowers with scarcely visible traces of anthers, and with the smallest corollas of all (No. 584, p. 131).

Visitors : A. Hymenoptera—*Apidae* : (1) *Apis mellifica*, L. ♀, s., very ab. ; (2) *Andrena albicans*, K. ♀, freq. B. Diptera—(a) *Syrphidae* : (3) *Eristalis arbustorum*, L., s. ; (4) *Rhingia rostrata*, L., f.p. ; (b) *Tipulidae* : (5) *Tipula*, sp., s. C. Lepidoptera—*Rhopalocera* : (6) *Pieris napi*, L., s. D. Coleoptera—*Nitidulidae* : (7) *Meligethes*, very ab.

*Valeriana montana*, L., is gynodioecious, some plants having distinctly proterandrous, hermaphrodite flowers with a large corolla,

<sup>1</sup> Compare Sprengel, No. 702, pp. 65-67.

others having only female flowers with a small corolla. The latter retain their stamens in an apparently almost perfect form, but their anthers do not contain a single grain of pollen (609).

*Valeriana tripteris*, L., is diœcious. In this species also there are large-flowered and small-flowered plants, but the larger flowers are not hermaphrodite as in *V. montana*, but male only; they retain a style, but stigmatic papillæ are not developed (609).

These four species of *Valeriana* form an interesting series:—*V. officinalis*, with one kind of individual only, and proterandrous hermaphrodite flowers; *V. montana*, with large-flowered and small-flowered individuals, the anthers in the latter being abortive; *V. tripteris*, in a similar condition, but with the pistil in the large-flowered individuals rudimentary also; finally, *V. dioica*, also diœcious, but exhibiting four different kinds of individuals (609).

*Valeriana cordifolia*, L., is distinctly proterogynous, according to Ricca (665).

*Centranthus ruber*, D.C., and *Fedia cornuœcopiæ*, are distinctly proterandrous, according to Delpino (178).

*Valerianella olitoria*, Much.—I have found this plant visited by four Coleoptera, eighteen Diptera, one Hemiptera, eleven Apidæ, and two Lepidoptera (590, III).

#### ORD. DIPSACEÆ.

*Morina elegans*.—The stigma is developed at the same time as the anthers, but overtops them, so that insect-visitors touch first the stigma and then the anthers, and usually effect cross-fertilisation. In the absence of insects the stigma curls inwards so as to touch the anthers and lead to self-fertilisation (356).

210. *DIPSACUS SILVESTRIS*, L.—The tube is 9 to 11 mm. long; the flower is markedly proterandrous; the style divides into two branches, whose inner surfaces are closely covered with stigmatic papillæ, but one of which is always partly, and sometimes entirely, aborted. The bracts stand up from the convex head as stiff, sharp spines; they distinctly overtop the anthers and stigmas and prevent them from being touched by the ventral surface of a bee creeping over the inflorescence. The anthers and stigmas are only touched by the bee's head as it is inserted in the flower; and in this process one stigma is in the way of the other, and the whole stigmatic surface of one is much more thoroughly rubbed by the bee's head when the other is absent. We seem to have here in

the abortion of one stigma an adaptive modification in progress and not yet perfected.

- (1) *Bombus rupestris*, L. ♀ (12—14); (2) *B. lapidarius*, L. ♂ ♀ (8—14), ab., (♂ as late as October 2); (3) *B. agrorum*, F. ♀ ♀ (12—15), all three species sucking. See also No. 590, III.

211. *SCABIOSA (KNAUTIA) ARVENSIS*, L.—In fine weather the flowers, owing to their great conspicuousness and their easily accessible honey and pollen, are visited by very miscellaneous insects in great numbers. Cross-fertilisation is ensured by markedly proterandrous dichogamy, and in the unlikely event of insect-visits not taking place, self-fertilisation is very unlikely to occur.

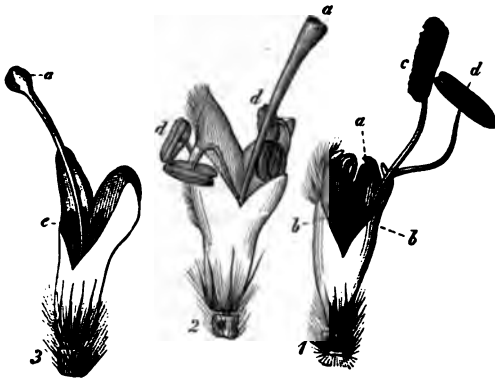


FIG. 108.—*Scabiosa arvensis*, L.

- 1.—Hermaphrodite flower in first (male) stage, after removal of one lobe of the corolla ( $\times 3\frac{1}{2}$ ).  
 2.—Ditto, in second (female) stage.  
 3.—Female flower, after removal of one lobe of the corolla.  
 a, stigma; b, anther still within the flower; c, ditto, dehiscing; d, ditto, empty and shrivelling  
 c, abortive anther.

About fifty flowers unite in a capitulum which may be hemispherical or only slightly convex, and become gradually larger from the centre to the margin by an increasing development of the outer lobe of the corolla. While in the central florets the tube is only 4 to 6 mm. long, and the lobes of the corolla, which are all similar, only 3 to 4 mm. long, in the marginal florets the tube is 7 to 9 mm. long, the external lobe of the corolla 6 to 11 mm., each of the two lateral lobes 4 to 7 mm., and the internal lobe only 3 to 4 mm. long.

In spite of the length of the tube the honey is easily accessible to a very large number of insects of the most various orders; for

easily accessible, for the stamens, which are at the bud, straighten themselves after the flower is 4 to 5 mm. beyond the tube, with the pollen-anthers directed upwards. Thus the flower offers to insects whether in quest of honey or of pollen that the close aggregation of the flowers prevents passing from one to another. Honey-seeking insects make repeated visits to the same capitulum, the development of the florets and by the length of time they secrete honey; pollen-seeking insects repeat their visits, because the anthers in the capitulum develop simultaneously but one by one (Fig. 10).

The style elongates after all the stamens have matured; its immature stigma stood previously in the tube but now protrudes 4 to 5 mm. from the corolla tube (a, 2). The empty anthers, if they have been visited by the insects, as frequently happens, are retracted into the flower by the filaments shrivelling up. After the capitulum the florets open and the anthers develop from the circumference towards the centre; the styles begin to elongate and the stigmas to develop. When all on the capitulum have completed their development, the stigmas almost simultaneously throughout the capitulum mature. The whole capitulum is at first male, and later, when cross-fertilisation takes place, wholly female, cross-fertilisation takes place between separate capitula in case of insect-visitation. The stigmas on a capitulum develop simultaneously and succeed each other very gradually, cross-fertilisation

If these female plants flowered earlier than the hermaphrodites, so that their stigmas were mature cotemporaneously with the anthers of the first hermaphrodites, then their origin might be explained on the principle of economy, as a saving of the first stamens which have no stigmas to fertilise. If the female capitula were less conspicuous than the others, the same explanation might be applied in this case as I have put forward in describing *Thymus* and *Glechoma*. But here neither the one fact nor the other is true ; but the female heads are just as conspicuous as the others and develop cotemporaneously with them. I can only account for their existence by the very great difference between the duration of the stigmas in the hermaphrodite capitula and the length of time that the anthers are covered with pollen.

It is of special importance for *Scabiosa arvensis* that the anthers on the same head should develop gradually throughout several days, and that the stigmas should ripen all on the same day, almost simultaneously. For owing to the first character there is never a lack of pollen, and owing to the second, as soon as a few sunny hours occur and bring out the insects, in a very short time all the stigmas on a capitulum are fertilised with pollen from another. Both characters together are therefore of use to the plant in the changeable and often continuously rainy weather of our summers. But when a spell of sunny weather appears the number of hermaphrodite flowers in the male condition must always be much greater than in the female condition ; the pollen of many heads must be wasted, and it must be an advantage to the plant if in some cases the stamens are aborted and the stigmas come so much the quicker to maturity. As every character of advantage for the maintenance of the species, which appears accidentally as an abnormality, can and must be retained by natural selection, so in *Scabiosa arvensis*, abortion of the stamens, occurring accidentally in certain plants, must have been perpetuated and intensified.

The power of self-fertilisation is not quite lost in the hermaphrodite plants ; for in capitula allowed to flower in the house and left untouched, many of the stigmas as they grow up may be seen to come in contact with anthers still dusted with pollen. But as a rule insect-visits are so numerous that self-fertilisation can only come into action in long-continued bad weather.

Visitors : A. Hymenoptera—(a) *Apidae* : (1) *Apis mellifica*, L. ♀ (6), ab., s., more rarely c.p. ; (2) *Bombus hortorum*, L. ♂ ♀ (17—21) ; (3) *B. terrestris*, L. ♀ ♂ (7—9) ; (4) *B. lapidarius*, L. ♀ (10—12) ; (5) *B. pratorum*, L.

♀ ♂ ♂ (8—11); (6) *B. Rajellus*, Ill. ♂ (10); (7) *B. agrorum*, F. ♀ (12—15); (8) *B. hypnorum*, L. ♂; (9) *B. silvarum*, L. ♀ ♀ (12—14); (10) *B. rupestris*, L. ♀ (12—14); (11) *B. vestalis*, Fourc. ♀ (12); (12) *B. campestris*, Pz. ♀ ♂ (10—12); (13) *B. Barbutellus*, K. ♂ ♀ (12); all these humble-bees only s.; (14) *Andrena Hattorfiana*, F. ♂ ♀ (6—7), s. and c.p.: it confines itself almost exclusively to this flower, and I have only once taken a male on *Jasione montana*, and again, a female on *Dianthus Carthusianorum*, s.; (15) *Andrena Gwynana*, K. ♀ (2½), c.p.; (16) *Halictus albipes*, F. ♀; (17) *H. leucozonius*, Schk. ♂ (4); (18) *H. cylindricus*, F. ♀ ♂ (3—4); (19) *H. sexnotatus*, K. ♀ (4); the species of *Halictus* sometimes s., sometimes c.p.; (20) *Nomada Fabriciana*, L. ♀; (21) *N. lineola*, Pz. ♀ ♂ (6); (22) *N. Jacobaeae*, Pz. ♀; (23) *N. armata*, Schaeff. ♀; (24) *Megachile Willughbiella*, K. ♂; (25) *M. maritima*, K. ♂ ♀, freq.; (26) *M. circumcincta*, K. ♀ ♂; (27) *M. centuncularis*, L. ♂; (28) *Diphysis serratulæ*, Pz. ♀ ♂, very ab., like all the species of *Nomada* and *Megachile*, only sucking; (29) *Osmia fulviventris*, Pz. ♀, c.p.; (30) *O. ænea*, L. ♂, s.; (31) *Cœlioxys quadridentata*, L. ♂ ♀, ab.; (32) *C. conoidea*, Ill. ♀; (33) *Heriades truncorum*, L. ♂; (34) *Stelis breviscula*, Nyl. ♂, the last four species, s.; (b) *Sphingidae*: (35) *Bembex rostrata*, L. (7); (36) *Psammophila affinis*, K. ♀ (5); (37) *Ps. viatica*, L. ♂ (4), all s.; (c) *Vespidæ*: (38) *Odynerus parietum*, L. ♀ (3), s. B. Diptera—(a) *Empidæ*: (39) *Empis tessellata*, F. (3, 4); (40) *E. livida*, L. (2½—3), both very ab., s.; (b) *Syrphidæ*: (41) *Eristalis tenax*, L. (7, 8); (42) *E. arbustorum*, L. (4, 5); (43) *E. nemorum*, L.; (44) *E. intricarius*, L.; (45) *Rhingia rostrata*, L. (11, 12); (46) *Volucella bombylans*, L.; (7, 8); (47) *V. plumata*, L.; (48) *V. pellucens*, L. (Sld.), all these *Syrphidæ* ab., s. and f.p.; (49) *Syrphus ribesii*, L. (3, 4), f.p.; (c) *Conopidæ*: (50) *Sicus ferrugineus*, L., ab., s.; (d) *Muscidæ*: (51) *Echinomyia tessellata*, F.; (52) *Ocyptera cylindrica*, F.; (53) *Micropalpus fulgens*, Mgn., all three s. C. Lepidoptera—(a) *Rhopalocera*: (54) *Colias hyale*, L. (Th.), ab.; (55) *Vanessa urticæ*, L. (12); (56) *Satyrus Janira*, L.; (57) *S. Medea*, S. V. (Sld.); (58) *Papilio Machaon*, L. (18); (59) *Hesperia lineola*, O.; (b) *Sphingidæ*: (60) *Zygæna loniceræ*, Esp. (Th.), ab.; (61) *Ino statice*, L.; (c) *Noctuæ*: (62) *Mamestra serena*, S. V. ♀ (Th.); (63) *Euclidia glyphica*, L.; (d) *Tineina*: (64) *Adela* sp., very ab., sometimes as many as four on one capitulum. D. Coleoptera—(a) *Nitidulidæ*: (65) *Meligethes*, ab., f.p.; (b) *Phalacridæ*: (66) *Olibrus bicolor*, F., f.p.; (c) *Lamellicornia*: (67) *Hoplia philanthus*, Sulz. (Sld.), feeding on the organs of the flower; (68) *Trichius fasciatus*, L., very ab., feeding on the tissues and also pairing on the flowers; (d) *Cerambycidæ*: (69) *Toxotus meridianus*, L., (Siebengeb.); (70) *Pachyta octomaculata*, F. (Sld.); (71) *Strangalia atra*, F., (Siebengeb.); (72) *Str. armata*, Hbst. (Siebengeb.); (73) *Str. attenuata*, L.; (74) *Str. melanura*, L.; (75) *Leptura livida*, F.: these *Cerambycidæ* feed on pollen and on the anthers, and those with small heads, especially *Str. attenuata*, also suck honey; (e) *Chrysomelidæ*: (76) *Cryptocephalus sericeus*, L., feeding on the parts of the flower

Altogether, I have observed upon *Scabiosa arvensis*, L. :—

	Apidae.	Lepidoptera.	Diptera.	Other Insects.	Total.
In Low Germany ...	45	19	17	20	101
On the Alps... ..	10	22	9	4	45

That is to say, in each hundred species of visitors we have :—

	Apidae.	Lepidoptera.	Diptera.	Other Insects.	Total.
In Low Germany ...	44·6	18·8	16·8	19·7	100
On the Alps... ..	22·2	48·9	20·0	8·9	100

(*Vide* No. 609, pp. 399, 400 : No. 590, III., pp. 76, 77.)

212. *SCABIOSA SUCCISA*, L.—The hemispherical capitulum consists of fifty to eighty florets, nearly equal in size, which develop in

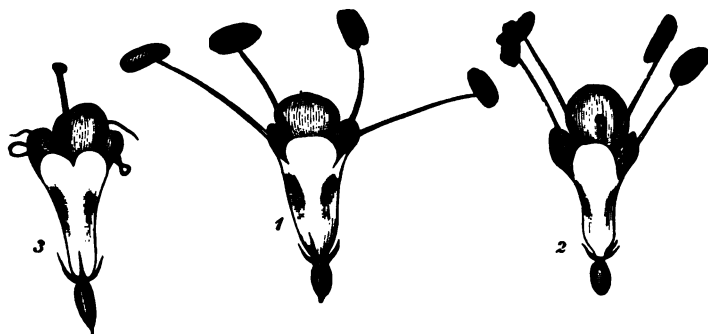


FIG. 109.—*Scabiosa succisa*, L.

- 1.—Flower, before dehiscence of the anthers (after removal of the epicalyx).
- 2.—Ditto, after the anthers have dehisced.
- 3.—Ditto, in female stage.

centripetal order. Honey is secreted by a small, fleshy ring above the ovary, surrounding the base of the style, and collects in the narrow, smooth base of the tube. The tube is 3 to 4 mm. long, and above the smooth honey-containing portion it is lined with

hairs to exclude rain. The honey is accessible to short-lipped insects, especially as the tube widens superiorly to a diameter of 2 mm. at the mouth, and the four (rarely five) rounded lobes of the corolla, of which the external is the largest, are easily thrust apart. On the damp, unproductive spots where *Scabiosa succisa* chiefly grows, its blue, hemispherical heads, about 20 mm. in diameter, are among the most conspicuous flowers; and in sunny weather until the middle of September, they are visited by very numerous insects, and are regularly cross-fertilised owing to their protandrous dichogamy. When the flower opens the stamens which were bent inwards in the bud straighten themselves one by one; then, while as yet the style scarcely extends beyond the mouth of the corolla (Fig. 109, 2), the anthers dehisce in succession; only when the stamens are completely withered, and the anthers, if insect-visits have taken place, are shaken off (Fig. 109, 3), does the style attain its full length, and the stigma, a little later, becomes viscid. Self-fertilisation can therefore only occur exceptionally, if at this time an anther, still dusted with pollen, comes by accident in contact with the stigma. In plants flowering in my room I have observed this to take place not unfrequently, but never in the open air.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s. and c.p., ab.; (2) *Bombus silvarum*, L. ♀ ♀ ♂ (as late as Oct. 7); (3) *B. lapidarius*, L., ♀ ♂; (4) *B. agrorum*, F. ♀ ♂ (both as late as Oct. 15, 1871); (5) *B. senilis*, Smith, ♀ ♂; (6) *B. terrestris*, L. ♀ ♂; (7) *B. pratorum*, L. ♀; (8) *B. vestalis*, Fourc. ♀ ♂; *B. rupestris*, L. ♂ (Oct. 15, 1871), all very ab., s.; (10) *Andrena Cetii*, Schrank. ♀, c.p.; (11) *A. convexiuscula*, K. ♂; (12) *Halictus rubicundus*, Christ. ♀, c.p.; (13) *H. leucozonius*, Schrank. ♂; (14) *H. cylindricus*, F. ♂, all freq. B. Diptera—(a) *Bombylidae*: (15) *Exoprosopa capucina*, F., ab. in July; (b) *Syrphidae*: (16) *Helophilus pendulus*, L., ab., also pairing on the flowers (Sept. 4, 1870); (17) *Eristalis arbustorum*, L.; (18) *E. nemorum*, L.; (19) *E. tenax*, L. (beginning of November) all ab., s. and f.p.; (20) *E. intricarius*, L., scarcer; (21) *Syrphus pyrastris*, L., s. and f.p.; (22) *Rhingia rostrata*, L., s.; (c) *Empidae*: (23) *Empis livida*, L., s., very ab.; (d) *Muscidae*: (24) Species of *Lucilia*; (25) *Musca cornicina*, F. C. Lepidoptera—(a) *Rhopalocera*: (26) *Pieris rapæ*, L., ab.; (27) *Satyrus Janira*, L.; (28) *Polyommatus Phlœas*, L., very ab.; (b) *Noctua*: (29) *Plusia gamma*, L., ab.; (c) *Crambina*: (30) *Botys purpuralis*, L., all s. D. Coleoptera—*Chrysomelidae*: (31) *Cryptocephalus sericeus*, L., feeding on the organs of the flower. See also No. 590, III.

This species, also, has been shown to include female as well as hermaphrodite plants in England by Darwin (167), in France by Lecoq,<sup>1</sup> and in Germany by Magnus (449).

*S. atropurpurea*, L., also, is gynodioecious (167).

<sup>1</sup> *Géographie botanique*, 1857, vi.

213. *SCABIOSA COLUMBARIA*, L.—This species for the most part resembles *S. arvensis* in the structure of its flower, but besides the five-lobed corolla it presents the following noteworthy differences. In *S. arvensis* the florets increase in size from the centre to the circumference of a capitulum, but in *S. Columbaria* this gradual increase is much less marked, though in the marginal florets the lobes of the corolla are large and conspicuous. Thus in one specimen, which I examined closely, the tube in the marginal flowers was 6 mm. long and 2 to 2½ mm. wide at the mouth; the external lobe of the corolla was 7 to 8 mm. long, the lateral were 6 mm., the internal 2 to 3 mm. In the florets of the disk, immediately contiguous to these marginal florets, the tube was 5 mm. long and 2 mm. wide at the mouth, and the lobes of the corolla were respectively 3, 2, 1½ mm. long; finally, in the central florets of the capitulum the tube was still 4 mm. long and 1½ mm. wide at the mouth, and the lobes of the corolla were 1 to 2 mm. long. In consequence of the smaller size of the central florets and the slight increase of size from the centre towards the margin, many more florets find room on equal space in *S. Columbaria* than in *S. arvensis*. So, although the capitula in *S. Columbaria* are distinctly smaller than in *S. arvensis*, they contain half as many florets again (seventy to eighty).

I have never found plants with abortive stamens in *S. Columbaria*.

This species only occurs near Lippstadt, in one locality and in small amount, so I have had little opportunity of watching its insect-visitors.

A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s., ab.; (2) *Bombus lapidarius*, L. ♂, very freq., s. B. Diptera—(a) *Syrphidae*: (3) *Eristalis tenax*, L.; (4) *E. nemorum*, L.; (5) *Helophilus trivittatus*, F., all three species ab., s., and f.p.; (b) *Conopidae*: (6) *Sicus ferrugineus*, L., s. A list of Alpine visitors (six flies, eight bees, and twenty-eight Lepidoptera) is given in No. 609, p. 400.

*Scabiosa lucida*, Vill., is visited by butterflies and *Syrphidæ* (609).

#### ORD. COMPOSITÆ.

The numerical preponderance which this family has attained in species and genera,<sup>1</sup> and the extreme abundance of many of the species, are due to the concurrence of several characters, most of

<sup>1</sup> In Dr. Ludwig Pfeiffer's *Synonymia Botanica* over 10,000 genera of Phanerogams are enumerated; of these, over 1,000 belong to the Compositæ.

which, singly, or in some degree combined, we have become acquainted with in other families, but never in such happy combination as in the Compositæ. The following points deserve special mention: (1) the close association of many flowers; (2) the accessibility of the honey, as well as its plentiful secretion and its security from rain; (3) the possession of a pollen-mechanism, which renders cross-fertilisation certain in the event of insect-visits.

1. The association of many flowers in one head is advantageous, for the following reasons:

(a) The flowers are rendered much more conspicuous, and are accordingly more visited by insects. Conspicuousness is in most cases increased still further either by the florets being directed outwards (*Cynaroideæ*), or by the limb of the corolla developing into a long lobe directed outwards, both of which phenomena become more marked towards the margin of the capitulum; or by the marginal florets becoming large coloured radiating laminæ, at the expense of the stamens or of both stamens and pistil (*Asteroideæ*); or, finally, by the innermost bracts performing this function (*Carlina*).

(b) Insects can fertilise numerous flowers with much less loss of time than when the flowers are separate; and so the chance of being fertilised is increased for every flower in the same ratio. The florets of the disk usually constitute a flat surface over which the insect crawls, and from which the reproductive organs protrude far enough to permit simultaneous fertilisation of many florets.

(c) As the involucre of the whole capitulum plays the part of a calyx in protecting the flowers, the calyces of the separate florets can be dispensed with entirely, or they may be adapted for a new and important purpose by being transformed into structures which aid the dispersion of the seeds by the wind, or into barbs furnished with recurved hooks (*Bidens*), which aid the transport of the seeds by animals.

2. The free accessibility of the honey is a character which most Compositæ share with Umbelliferae; and, accordingly, the two orders rival one another in the variety of their insect-visitors (vide *Cirsium arvensis*). But while in Umbelliferae the honey lies fully exposed to the rain upon the fleshy disk which secretes it, in Compositæ it is secreted by a ring surrounding the style at the base of a narrow tubular corolla, and as it accumulates it rises up into the wider part of the corolla where it is accessible to the most short-lipped insects, and where the anthers shelter it from rain.

Thus, while the flat layer of honey in Umbelliferae is only suitable for short-lipped insects, the honey of Compositae is not only accessible to them but may be sucked by Lepidoptera and bees also.

3. The pollen-mechanism agrees essentially with that of Lobeliaceae. The anthers cohere to form a hollow cylinder, and dehisce introrsely, filling the cylinder with pollen, before the flower opens. The two stigmas lie at first closely applied together in the lower part of the anther-tube, and as the style grows they brush the pollen out of the tube by means of the hairs on their outer surface. So in the first period the pollen is exposed to insect-visitors, and in the second the stigmas separate and expose their papillar surfaces.

The arrangement of the hairs and of the stigmatic papillae shows some diversity in Composites. The former sometimes, as in Lobeliaceae, sweep the pollen before them, forming a simple ring round the style at the base of the stigmas (*e.g. Centaurea, Cirsium*), or aggregated in a tuft at the extremity of the stigmas (*e.g. Achillea, Chrysanthemum*); sometimes they are spread over more or less of the surface of the style, and the pollen remains entangled among them (*e.g. Leontodon*). The stigmatic papillae sometimes wholly or partially cover the inner surfaces of the stigmas, and sometimes are restricted to broader or narrower areas at the margin. This sweeping mechanism, which is apparently inherited from Lobeliaceae, is perfected in many Compositae by a peculiar irritability of the filaments, which contract when touched by an insect's proboscis and draw the anther-tube downwards, squeezing the pollen out at the upper end exactly at the proper time for it to be carried to other flowers.

Cross-fertilisation in case of insect-visits is thoroughly ensured for the separate florets in the same way as in Lobeliaceae, and it is rendered in many cases very probable, and in others inevitable, for the inflorescence as a whole. For in all cases in which the development of the hermaphrodite flowers progresses so slowly from the margin of the capitulum towards its centre that one or more rows of florets in the female stage are always surrounded by several rows in the male, the crossing of separate capitula must at least be effected by all insects which alight at the margin (*Bellis, Chrysanthemum*, etc.); but in many Cynareae the florets open centripetally in such quick succession that the capitulum is for a time male only, and afterwards for some time

female only, and in this case all insect-visitors must lead to the crossing of separate capitula (*Carduus*). Lastly, in the few Compositæ in which the florets are all unisexual, either the male and female florets are confined to separate capitula or the outer florets in all the capitula are female and the inner male (*Calendula*, *Silphium*, etc.). In the former case the crossing of separate capitula is obviously inevitable, and in the latter (since the outer florets develop first) it is probable, and more so than in the case described where centripetal development proceeds slowly in a capitulum of hermaphrodite florets.

In absence of insects self-fertilisation is often rendered possible in the hermaphrodite flowers by the stigmas curving backwards till their papillæ come in contact with the pollen.

The irritability of the filaments in *Centaurea*, *Onopordum*, *Cichorium*, *Hieracium*, etc., was observed more than a hundred years ago by Koelreuter (396, Pt. III). Severin Axell gives a *résumé* of more recent observations on this point by Morren, Cohn, Unger, and others (17).

Sprengel recognised the significance of the enlarged marginal florets, the closing of the capitulum during rain, the brushes on the style or stigmas, and the distinct proterandry (702, pp. 365-384).

Hildebrand made the floral mechanism of Compositæ, especially the distribution of the brushes and the stigmatic papillæ, the subject of a very elaborate paper containing many magnified figures of styles (357). In the same year (1869) Delpino gave a full account of the adaptive modifications of Compositæ (178), and appended some notes on the bees seen by him visiting Compositæ. In a more recent work (180) he tries to prove the genetic connection of Compositæ with Campanulaceæ and Lobeliaceæ, and to trace the gradual passage from entomophilous *Senecionidæ* to distinctly anemophilous *Artemisiaceæ*. I am unacquainted with most of the forms which Delpino treats of, and am therefore unable to criticise his conclusions, so I confine myself to a general reference to his interesting research.

#### Tribe *Eupatoriaceæ*.

Müller tells me by letter that at Itajahy, at the borders of woods, is the haunt of *ulæ*.

**M. CANNABINUM, L.**—The capitulum contains four florets, in each of which the tube is

2½ mm. long, and the wider throat 2 mm. long in addition. By themselves the capitula are small and insignificant, but very many (usually several hundred) are closely aggregated in an inflorescence. The red-bordered bracts, the reddish corollæ of the florets, and the white projecting stigmas give this inflorescence a reddish-white appearance. In this plant the divisions of the style are quite as

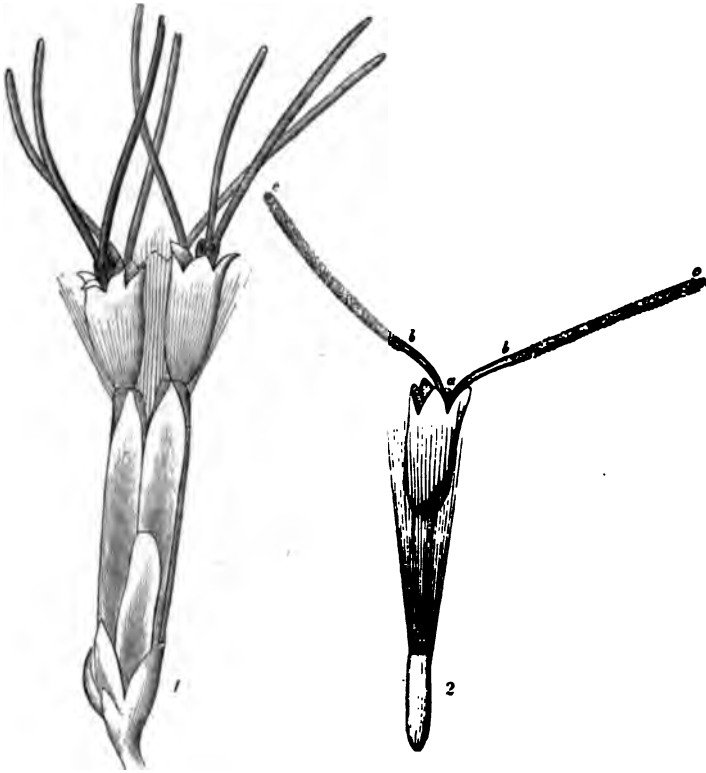


FIG. 110.—*Eupatorium cannabinum*, L.

1.—A capitulum of four florets, in their first (male) stage.

2.—A single floret, in second (female) stage.

From *a* to *b* each branch of the style bears a strip of stigmatic papillæ on each edge; from *b* to *c* it is clothed with hairs.

long as the whole corolla (5 mm.). They are furnished with rows of stigmatic papillæ along their edges, only for the first quarter of their length (*a, b*, Fig. 110, 2); for the remaining three-quarters they are thickly clothed all round with hairs. In the first period the lower stigmatic part of the branches of the style remains still inclosed in the anther-cylinder (Fig. 110, 1); the ends, furnished with

hairs, project beyond it, and diverge so widely that insect-visitors come in contact with them all round, and carry off upon their hairy or scaly coats the pollen that had been entangled in the hairs of the styles. Afterwards, the lower stigmatic portions emerge from the anther-cylinder and from the throat of the corolla (Fig. 110, 2), and they too diverge so widely that an insect in obtaining its honey must come in contact with them. Cross-fertilisation is thus ensured, if insect-visits have taken place to a sufficient extent to clear all the pollen from the hairs of the style before the stigmas in the same floret are exposed. But if these hairs still bear pollen when the stigma becomes exposed, an insect-visitor may effect self-fertilisation as easily as cross-fertilisation. If no insects visit the flower at all, fertilisation and even cross-fertilisation are still possible, for the outspread branches of the style sometimes come in contact with the stigmas of neighbouring florets.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s.; (2) *Bombus* (*Apathus*) *vestalis*, Fourc. ♂, s. B. Diptera—(a) *Syrphidae*: (3) *Eristalis arbustorum*, L.; (4) *E. nemorum*, L.; (5) *E. tenax*, L., all three species, ab., f.p.; (b) *Muscidae*: (6) *Echinomyia fera*, L.; (7) *Dexia canina*, F.; (8) *Lucilia albiceps*, Mgn. C. Lepidoptera—*Rhopalocera*: (9) *Pieris rapæ*, L.; (10) *Thecla quercus*, L.; (11) *Lycæna*, sp.; (12) *Vanessa Io*, L., ab.; (13) *Argynnis Paphia*, L., ab.; (14) *Satyrus Galatea*, L.; (15) *S. Medusa*, S. V.; (16) *S. Egeria*, L.; (17) *Hesperia lineola*, O. I saw all these butterflies together sucking the flowers of *Eupatorium* on a sunny slope near Willebadessen (August, 1871): they took no heed of other neighbouring flowers. D. Neuroptera—(18) *Panorpa communis*, L. This list is very remarkable on account of the preponderance of butterflies. See also No. 590, III.

#### Tribe *Asteroideæ*.

215. *SOLIDAGO VIRGA-AUREA*, L.—In the florets of the disk the style is identical with that of *Chrysocoma* (cf. Hildebrand, 357). But while in *Chrysocoma* numerous capitula unite to form one surface, and can therefore dispense with ligulate marginal florets, in *S. virga-aurea* the capitula are distributed over an elongated axis; and the disk of each capitulum (4 to 5 mm. in diameter) is rendered conspicuous by five to seven golden-yellow marginal florets which increase the whole diameter of the capitulum to 14 or even 19 mm. The marginal florets have acquired their excessive development of corolla at the expense of their stamens, which are quite absent; the branches of the style have almost entirely lost their useless sweeping-hairs, and bear stigmatic papillæ along the whole length of both borders of their inner surfaces.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, s., ab.; (2) *Bombus rupestris*, L. ♂, s.; (3) *B. campestris*, L. ♂, s.; (4) *B. terrestris*, L. ♂, s.; (5) *Andrena denticulata*, K. ♀ ♂, c.p. and s. (Tekl. Borgst.). B. Diptera—*Syrphidæ*: (6) *Eristalis arbustorum*, L.; (7) *E. nemorum*, L., both species f.p., ab. C. Lepidoptera—*Rhopalocera*: (8) *Thecla ilicis*, Esp., s. A list of Alpine visitors (six bees, twenty-two flies, twenty-seven Lepidoptera) is given in my *Alpenblumen* (No. 609).

## 216. SOLIDAGO CANADENSIS, L.:—

Visitors: Diptera—(a) *Syrphidæ*: (1) *Eristalis arbustorum*, L.; (2) *E. nemorum*, L.; (3) *Syritta pipiens*, L., all three species f.p., ab.; (b) *Muscidæ*: (4) *Sarcophaga carnaria*, L., f.p.; (5) Numerous small *Muscidæ*. See also No. 590, III.

217. *BELLIS PERENNIS*, L.—Numerous tiny florets 1 to 2 mm. in length unite to form a flat, yellow disk 6 mm. in diameter. The white outer lobes (5 mm. long) of the marginal florets bring the diameter of the whole capitulum up to 16 mm. The marginal florets have no stamens, and their styles have lost their sweeping-hairs; the two branches of the style are furnished with stigmatic papillæ on their edges for their whole length (cf. Hildebrand, 357). On the other hand, in the florets of the disk the style is short, broadly oval, and closely covered with sweeping-hairs on the outer surface from the broadest part to the tip; these hairs both sweep the pollen out of the anther-cylinder as the style elongates, and afterwards hold it until it is removed by insects. The branches of the style in the disk-florets are only furnished with a short strip of stigmatic papillæ on each border below the broadest part. After fertilisation the branches of the style are again drawn within the corolla, so that the placing of more pollen on the already fertilised stigma is avoided.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, c.p., freq.; (2) *Andrena parvula*, K. ♀, c.p.; (3) *Halictus minutissimus*, K. ♀, c.p., freq.; (4) *H. cylindricus*, F. ♀, s.; (5) *Sphecodes gibbus*, L. ♀, s.; (6) *Nomada lineola*, Pz. ♂, s.; (7) *N. flavoguttata*, K. ♂, s.; (8) *Osmia rufa*, L. ♀, s. and c.p.; (b) *Formicidæ*: (9) *Myrmica lævinodis*, Nyl., tried to suck. B. Diptera—(a) *Empidæ*: (10) *Empis livida*, L., s., very ab.; (11) *E. opaca*, F., s.; (b) *Syrphidæ*: (12) *Eristalis arbustorum*, L.; (13) *E. sepulcralis*, L.; (14) *E. tenax*, L.; (15) *E. pertinax*, Scop.; (16) *Rhingia rostrata*, L., all five species f.p., very ab.; (17) *Syritta pipiens*, L., f.p. and s., ab.; (18) *Melithreptus scriptus*, L., f.p.; (c) *Muscidæ*: (19) *Scatophaga stercoraria*, L.; (20) *Sc. merdaria*, F., both species f.p., ab.; (21) *Lucilia cornicina*, F., f.p., freq.; (22) *Musca corvina*, F., do. All these flies had their tongues, legs, and under surface, especially of the thorax, thickly coated with pollen. C. Lepidoptera—*Rhopalocera*: (23) *Satyrus pamphilus*, L., s.; (24) *Polyommatus dorilis*, Hufn., s.

*Muscidæ* : (8) *Ocyptera cylindrica*, F., s. C. Lepidoptera—(a) *Rhopalocera* : (9) *Polyommatus dorilis*, Hfn. ; (10) *Lycæna alsus*, W. V. ; (b) *Noctuæ* : (11) *Plusia gamma*, L., all three s.

#### Tribe *Inuloideæ*.

222. *GNAPHALIUM LUTEOALBUM*, L., as a rule only comes into bloom at Lippstadt in September. On the wet, sandy places where it grows, it is by far the most conspicuous plant, especially as it grows associated in considerable numbers. One sunny day at noon (Sept. 29, 1869) I noticed the following insects upon its capitula :—

Visitors : A. Hymenoptera—(a) *Apidæ* : (1) *Sphecodes gibbus*, L. ♂ ♀, several varieties including *ephippia*, L., s. ; (2) *Halictus sexsignatus*, Schenck, ♂ ♀, s. ; (b) *Sphegidæ* : (3) *Pompilus viaticus*, L., s. ; (4) *Ceropales maculata* F., s. B. Diptera—(a) *Syrphidæ* : (5) *Melithreptus scriptus*, L. ; (6) *Melanostoma mellina*, L., both f.p. ; (b) *Muscidæ* : (7) *Lucilia*, freq. ; (8) *Pollenia rudis*, F., both f.p.

*Gnaphalium uliginosum*, L.—On the inconspicuous capitula of this plant I once caught *Sphecodes ephippia*, L., s.

223. *PULICARIA DYSENTERICA*, Gärtn.—The disk of the capitulum consists of more than 600 florets. Each floret has a tube about 4 mm. long, narrow below and wider above, terminating in five triangular teeth. I could not discover that the honey rose up into the wider part of the tube, but even without its doing so it is accessible to moderately short-lipped insects. In these florets of the disk no part of the style, except its two stigmatic branches, protrudes from the anther-cylinder. The stigmas spread apart horizontally, close above the corolla, in the same spot where the pollen lay in the first stage, so that here also many florets can be fertilised simultaneously by an insect-visitor. The branches of the style are covered over their whole inner surfaces with stigmatic papillæ, and on the upper third of their outer surfaces with hairs which point obliquely upwards. Along the edges of the triangular valves which form the upper end of the anther-cylinder stand unicellular hairs, which are much longer and thicker than the sweeping-hairs on the style and which serve to hold the pollen that has been swept out of the anther-cylinder. The disk is surrounded by nearly 100 marginal florets, each of which has an outer golden-yellow lobe 5 to 7 mm. long ; in these the tube is 2 to 3 mm. long, and from it a style protrudes identical with that in

the florets of the disk, possessing even the sweeping-hairs that are here useless from the absence of stamens.

Visitors: A. Hymenoptera—*Apidae*: (1) *Heriades truncorum*, L. ♀ ♂, very freq., s. and c.p.; (2) *Halictus longulus*, Sm. ♂; (3) *H. maculatus*, Sm. ♂; (4) *H. albipes*, F. ♂; (5) *H. cylindricus*, F. ♂; (6) *H. nitidus*, Schenck, ♂, all s. B. Diptera—*Syrphidae*: (7) *Eristalis arbustorum*, L.; (8) *E. sepulcralis* L., both species, f.p., very ab.; (9) *Melithreptus scriptus*, L., f.p. C. Lepidoptera—(10) *Polyommatus doris*, Hfn.; (11) *Lycæna* sp.; (12) *Hesperia thauamas*, Hfn., s. D. Coleoptera—*Chrysomelidae*: (13) *Cassida muræa*, L., whose larva feeds on the leaves of this plant, often creeps about the flowers and effects cross-fertilisation.

#### Tribe *Helianthoideæ*.

*Zinnia*, my brother Fritz Müller tells me, is visited almost exclusively by Lepidoptera, especially *Hesperidae*, at Itajahy. In North America it is visited by ruby-throated humming-birds also (731).

224. *HELIANTHUS MULTIFLORUS*, L.—Delpino found *Helianthus* fertilised chiefly by *Heriades truncorum*, L., which tapped the flowers in their first (male) stage with its abdomen, and dexterously swept up the pollen that exuded from the anther-cylinder with its abdominal collecting-hairs; hence he concluded that the insect and the plant had been specially created for one another. The various relations of insects to flowers, as they are described in this book, prove such a conception to be untenable.

I have observed as visitors of *H. multiflorus*:—

A. Hymenoptera—*Apidae*: (1) *Megachile centuncularis*, F., c.p.; (2) *Halictus zonulus*, Sm. ♀, s. B. Diptera—*Syrphidae*: (3) *Eristalis tenax*, L.; (4) *Syrphus pyrastris*, L.; (5) *S. ribesii*, L., all three f.p. and s.

#### Tribe *Anthemideæ*.

225. *ACHILLEA MILLEFOLIUM*, L.—This plant is a very marked instance of the advantage of many small flowers being united together, both for attracting insects and for simultaneous cross-fertilisation of many flowers by a single insect-visitor.

In the florets of the disk, the corolla consists of a tube scarcely 2 mm. long, passing above into a throat 1 mm. long and equally wide, ending in five triangular teeth. Honey is secreted by an annular ridge (*b*, Fig. 112, 2) surrounding the base of the style,

and rises up into the throat and so is accessible to the most short-lipped insects. When the flower opens, the two divisions of the style are closely appressed and project into the lower part of the anther-cylinder which is filled with pollen (Fig. 112, 2). They are



FIG. 112.

1-5.—*Achillea Millefolium*, L.

1.—A capitulum, from above. *a*, stigmas of female flowers; *b*, stigmas of florets of the disk in their second stage; *c*, anther-cylinders of disk-florets in their first stage; *d*, bud about to open. Numerous younger buds are hidden in the centre of the capitulum.

2.—Floret of the disk, just expanding; in section. *e*, ovary; *f*, nectary, surrounding the base of the style; *g*, style; *h*, tube of corolla; *i*, filaments; *k*, two divisions of the style; *l*, tip of style, with its brush of hairs; *m*, anther-cylinder; *n*, throat of corolla; *o*, valves, closing the anther-cylinder.

3.—A disk-floret, slightly more advanced, with its bract; the pollen is issuing from the anther-cylinder.

4.—Older disk-floret. The stigmas are separate and exserted; the anthers have been withdrawn into the corolla by contraction of the filaments.

5.—Tip of style of a disk-floret in its first (male) stage. *k*, stigmatic papillae; *l*, sweeping-hairs; *p*, pollen-grains.

6-8.—*Chrysanthemum leucanthemum*, L.

6.—Disk-floret, in first (male) stage.

7.—Ditto, in second (female) stage.

8.—Tip of one stigmatic branch, seen from the inner side ( $\times 60$ ).

furnished at the tip with divergent hairs (5), so that as the style elongates the pollen is pressed out at the upper end of the anther-cylinder, whose terminal valves (*o*, 2) separate. Finally the two branches of the style emerge, spread apart, turning their stigmatic

inner surfaces upwards, and bend their hairy tips so far backwards and inwards that some of the pollen which remains adhering to them is removed from the chance of contact with insects (Fig. 112, 4). While the pollen is being forced up the anther-cylinder projects slightly beyond the corolla (Fig. 112, 3); when the stigmas are exposed, the anther-cylinder lies more deeply in the throat of the corolla, having been drawn down by the contracting filaments. The stigmas thus come to lie immediately above the corolla, in the same spot where the pollen was before. The result is that as the under-sides of insect-visitors sweep over the capitulum they come in contact with many florets and effect many cross-fertilisations at the same time. In this species, twenty or more florets (which, however, do not develop simultaneously, but centripetally) are united in a disk about 3 mm. in diameter; but since five florets at the margin have each an external lobe over 3 mm. long and rather more than 3 mm. broad, the diameter of the disk is increased to 9 or 10 mm. The marginal florets have attained this enormous development of the corolla at the expense of the stamens, which are quite absent; they possess a style however, which divides into two branches, covered on their upper surfaces with stigmatic papillæ but destitute of hairs. In spite of the enlargement of the corolla in the marginal florets, the capitula, when they stand alone, are not very conspicuous; but very many capitula, often more than one hundred, are united in a corymbose inflorescence, which is not only very conspicuous but permits still more extensive cross-fertilisation to be effected at once by an insect-visitor.

226. *ACHILLEA PTARMICA*, L., is distinguished from *A. Millefolium* by the much greater size of its separate capitula, which are, however, associated in much less numbers in an inflorescence. About eighty to over one hundred florets, each scarcely  $2\frac{1}{2}$  mm. long, are united in a disk 6 to 7 mm. in diameter, at whose edge eight to twelve marginal florets stand. Each of these latter possess an outer lobe 4 to 6 mm. long and not quite so broad, whereby the diameter of the attractive surface of each capitulum is increased to 15 or even 18 mm. In other points the flowers agree with those of *A. Millefolium*. Both plants grow in equal abundance in the same localities, they flower at the same time, and are visited to the same extent by the same insects. In both, but especially in *A. Millefolium*, the strong odour of the plants is probably a great additional attraction; for species of *Prosopis*, which are especially fond of

strong-smelling flowers, are often found in great numbers on both plants, particularly on *A. Millefolium*.

The following list of insects, which I have observed on the flowers of these *two species*, shows how successfully the attractive contrivances described and the easily accessible pollen and honey effect their purpose:—

A. Hymenoptera—(a) *Apidae*: (1) *Prosopis variegata*, F. ♀ ♂, very ab.; (2) *P. pictipes*, Nyl. ♀ ♂, both species s., and gathering pollen with their mouths; (3) *Sphecodes gibbus*, L., all varieties, including *ephippia*, L., ♀ ♂, s., ab.; (4) *Haliectus cylindricus*, F. ♀ ♂, c.p. and s.; (5) *H. maculatus*, Sm., c.p.; (6) *H. leucozonius*, K. ♀, c.p.; (7) *H. morio*, F. ♀, c.p.; (8) *H. villosulus*, K. ♀, c.p.; (9) *H. rubicundus*, Chr. ♂, s.; (10) *H. quadricinctus*, F. ♂, s.; (11) *Andrena fulvicrus*, K. ♀ ♂, c.p. and s., ab.; (12) *A. pilipes*, F. ♂, s.; (13) *A. dorsata*, K. ♀ ♂, c.p. and s., ab.; (14) *A. chrysosceles*, K. ♀; (15) *A. fuscipes*, K. ♂; (16) *A. nana*, K. ♂, s.; (17) *A. argentata*, Sm. ♂, s.; (18) *A. albicans*, K. ♂, s.; (19) *A. lepida*, Schenck, ♂, s.; (20) *A. nigripes*, K. ♀, s.; (21) *A. denticulata*, K. ♂, s.; (22) *Colletes fodiens*, K. ♀ ♂, c.p., f.p. and s., very ab.; (23) *C. Davieseana*, K. ♀ ♂, still more ab.; (24) *Nomada zonata*, Pz. ♀, s.; (25) *N. ruficornis*, L. ♀, s.; (26) *Stelis breviscula*, Nyl. ♀, s.; (27) *Heriades truncorum*, L. ♀ ♂, c.p. and s.; (28) *Chelostoma nigricorne*, Nyl. ♂, s.; (29) *Osmia spinulosa*, K. ♀, c.p.; (30) *O. leucomelæna*, K. ♀, c.p.; (b) *Sphegidae*: (31) *Crabro alatus*, Pz., Lep. ♀ ♂, ab.; (32) *Cr. subterraneus*, F. ♀; (33) *Lindenius albilabris*, F., freq.; (34) *Oxybelus bellus*, Dlb.; (35) *O. trispinosus*, F.; (36) *O. uniglumis*, L., Dlb., all three ab.; (37) *Philanthus triangulum*, F. ♀ ♂, freq.; (38) *Cerceris arenaria*, L. (v. d. L.), not rare; (39) *C. labiata*, F., ab.; (40) *C. variabilis*, Schrck., very ab.; (41) *Dinetus pictus*, F.; (42) *Ammophila sabulosa*, L.; (43) *Pompilus trivialis*, Kl. ♂; (44) *P. chalybeatus*, Schiödt, ♀; (45) *P. plumbeus*, Dhlb. ♀ ♂, (46) *P. rufipes*, L. ♀ ♂; (47) *P. viaticus*, L. ♂; (48) *Ceropales maculata*, F., freq.; (c) *Vespidæ*: (49) *Odynerus sinuatus*, F. ♀; (50) *O. parietum*, L. ♂; (51) *Pterocheilus phaleratus*, Latr. ♀; (d) *Chrysidæ*: (52) *Hedychrum lucidulum*, Latr., Dhlb. ♀ ♂, freq.; (e) *Tenthredinidæ*: (53) *Tenthredo notha*, Kl., s., very freq.; (54) *Tenthredo scrophulariæ*, L.; (55) Several undetermined sp. of *Tenthredo*. B. Diptera—(a) *Stratiomyidæ*: (56) *Odontomyia viridula*, F., ab.; (b) *Tabanidæ*: (57) *Tabanus rusticus*, L., freq.; (c) *Bombylidæ*: (58) *Exoprosopa capucina*, F., freq.; (d) *Empidæ*: (59) *Empis livida*, L., ab.; (e) *Syrphidæ*: (60) *Melithreptus scriptus*, L.; (61) *M. tæniatus*, Mgn.; (62) *Volucella bombylans*, L.; (63) *V. pellucens*, L. (Almethal); (64) *Eristalis sepulchralis*, L.; (65) *E. tenax*, L.; (66) *E. arbustorum*, L.; (67) *E. nemorum*, L., all four ab., both s. and f.p., usually covered below with pollen; (68) *Syritta pipiens*, L., s. and f.p., ab.; (69) *Eumerus sabulonum*, Fall.; (f) *Conopidæ*: (70) *Conops flavipes*, L.; (71) *Physocephala vittata*, F., both freq., s.; (g) *Muscidæ*: (72) *Gymnosoma rotundata*, Pz.; (73) *Ocyptera cylindrica*, F.; (74) *Echinomyia ferox*, Pz., freq.; (75) *E. tessellata*, F.; (76) *Gonia capitata*, Fallen. C. Lepidoptera—(a) *Rhopalocera*: (77) *Pieris napi*, L.; (78) *Hesperia silvanus*, Esp.; (79) *Satyrus pamphilus*, L.; (80) *Polyommatus Philæas*, L.; (81) *Lycæna Ægon*, S. V.; (b) *Crambina*: (82) *Botys purpuralis*, L., all s. D. Coleoptera—(a) *Buprestidæ*: (83) *Anthaxia nitidula*, L. (Thur.); (b) *Cerambycidæ*: (84) *Leptura testacea*,

L.; (85) *L. livida*, F., both f.p.; (c) *Coccinellidæ*: (86) *Exochomus auritus*, Scriba, ab.; (d) *Chrysomelidæ*: (87) *Cryptocephalus sericeus*, L., feeding on the tissues of the flower. Forty-three additional visitors (including fifteen beetles) are enumerated in No. 590, III. See also No. 609.

227. *ANTHEMIS ARVENSIS*, L.—The structure of the flower is similar to that of *Chrysanthemum leucanthemum* and *Matricaria Chamomilla*; in regard to conspicuousness and amount of insect-visits it stands between the other two. Each capitulum forms a white circle 21 to 27 mm. in diameter, with a central yellow disk 5 to 7 mm. in diameter. Since the plant does not possess the strong odour of *M. Chamomilla* it is visited by numerous bees.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, s.; (2) *Andrena Schrankella*, Nyl. ♀, c.p. and s.; (3) *A. nigroænea*, K. ♀, c.p. and s.; (4) *A. fulvicrus*, K. ♀, c.p. and s.; (5) *A. nana*, K. ♀, s.; (6) *A. minutula*, K. ♂; (7) *Halictus lucidulus*, Schenck, ♀; (8) *H. nitidiusculus*, K. ♀; (9) *Colletes Daviesæana*, K. ♀ ♂, c.p. and s., ab.; (b) *Sphegidæ*: (10) *Cerceris variabilis*, Schrk. ♂; (11) *Crabro cribrarius*, L. Dlb. ♀; (12) *Cr. alatus*, Pz. ♂ ♀; (c) *Tenthredinidæ*: (13) *Tenthredo notha*, Kl. B. Diptera—(a) *Stratiomyidæ*: (14) *Nemotelus pantherinus*, L., very ab.; (b) *Syrphidæ*: (15) *Eristalis arbustorum*, L.; (16) *E. nemorum*, L.; (17) *E. tenax*, L.; (18) *E. sepulcralis*, L., all four f.p., ab.; (19) *Syritta pipiens*, L.; (c) *Muscidæ*: (20) *Echinomyia tessellata*, F.; (21) *Scatophaga stercoraria*, L.; (22) *Sc. merdaria*, F., all three f.p. C. Coleoptera—(a) *Elateridæ*: (23) *Athous niger*, L.; (b) *Curculionidæ*: (24) *Bruchus* sp.; (c) *Cerambycidæ*: (25) *Leptura livida*, L.

228. *ANTHEMIS TINCTORIA*, L. (Thuringia, July, 1868 and 1870):—

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Colletes marginata*, L. ♂, s.; (2) *Halictus maculatus*, Sm. ♀, c.p.; (3) *Heriades truncorum*, L. ♀, s. and c.p.; (b) *Ichneumonidæ*: (4) Various sp. B. Diptera—(a) *Syrphidæ*: (5) *Eristalis arbustorum*, L.; (6) *Syritta pipiens*, L.; (7) *Melithreptus tæniatus*, Mgn., all three f.p.; (b) *Conopidæ*: (8) *Myopa* sp., s.; (c) *Muscidæ*: (9) *Gymnosoma rotundata*, L.; (10) *Ulidia erythrophthalma*, Mgn., in hundreds. D. Coleoptera—(a) *Elateridæ*: (11) *Agriotes gallicus*, Lap.; (b) *Mordellidæ*: (12) *Mordella fasciata*, F. Delpino mentions as a visitor of this plant *Lomatia Beelzebub*, F. (Diptera, Bombylidæ). (No. 178, p. 121.) The flowers are described and additional visitors are enumerated in No. 590.

229. *CHRYSANTHEMUM LEUCANTHEMUM*, L. (Fig. 112, 6—8). Four to five hundred florets, in which the corolla is scarcely 3 mm. long, unite to form a yellow disk 12 to 15 mm. in diameter; at its edge are twenty to twenty-five florets with abortive stamens, each of which has a white external lobe, 14 to 18 mm. long, 3 to 6 mm. broad, so that the yellow disk is surrounded by a white border as broad as or broader than itself, and the whole attractive surface now has a diameter of 40 or more millimetres. In the

florets of the disk, the throat, into which the honey rises, is scarcely 1 mm. deep, so that the honey is accessible to the most short-lipped insects. In the first stage (Fig. 112, 6), the pollen, and in the second (Fig. 112, 7), the stigmas, stand immediately above the corolla; insects moving over the capitulum must cross-fertilise many florets simultaneously. The branches of the style end in a thick tuft of divergent hairs (*l*, 8), which sweep the pollen out of the anther-cylinder (*p*, 6) as the style elongates. The inner surface of each division of the style bears two broad rows (*k'*, 8) of stigmatic papillæ, separated by a narrow interval; these stigmatic papillæ extend over the outer edges, and are there regularly dusted with pollen if the pollen which has got heaped above the anther-cylinder by the protruding style is not removed by insects. Self-fertilisation is as inevitable in absence of insects as cross-fertilisation is when their visits occur. The stigmatic surfaces in the marginal florets are just as in the florets of the disk; but the now functionless sweeping-hairs are distinctly shorter in the marginal florets.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Prosopis communis*, N. ♀; (2) *Sphecodes gibbus*, L. ♀ ♂, all varieties, including *ephippia*, L.; (3) *Halictus maculatus*, Sm. ♀ ♂, c.p. and s., freq.; (4) *H. leucozonius*, Schr. ♀, c.p.; (5) *H. albipes*, F. ♂, s.; (6) *H. cylindricus*, F. ♀ ♂, c.p. and s., very ab.; (7) *H. villosulus*, K. ♀ ♂, c.p. and s.; (8) *H. rubicundus*, Chr. ♀, c.p.; (9) *Andrena xanthura*, K. ♀, s.; (10) *A. nigroænea*, K. ♀, c.p.; (11) *Colletes Daviesiana*, K. ♀ ♂, c.p. and s., very ab.; (12) *Bombus terrestris*, L. ♂, s., once. (Here also Delpino's distinction between *Compositæ* adapted for *Halictus* and those adapted for bees with abdominal brushes falls to the ground, for though the flat disk of *Chrysanthemum leucanthemum* must, according to Delpino, be fertilised mainly or exclusively by bees with abdominal brushes, I found no such bees on it, but many specimens of *Halictus*, *Andrena*, and *Colletes*). (b) *Sphegidae*: (13) *Cerceris variabilis*, Schr.; (14) *Crabro cephalotes*, Shuck. ♀; (15) *Cr. cribrarius*, L., Dlb. ♂, freq.; (16) *Oxybelus uniglumis*, L., Dlb., ab.; (17) *O. trispinosus*, F.; (c) *Ichneumonidae*: (18) Various sp.; (d) *Tenthredinidae*: (19) *Tenthredo* (*Allantus*) *notha*, Kl., s.; (20) *T. scrophulariæ*, L.; (21) Several undetermined sp. of *Tenthredo*; (22) *Cimbex sericea*, L. B. Diptera—(a) *Empididae*: (23) *Empis rustica*, F., s.; (b) *Stratiomyidae*: (24) *Nemotelus pantherinus*, L., exceedingly abundant, sucking; (25) *Odontomyia viridula*, F., very ab., s.; (c) *Bombyliidae*: (26) *Systoechus sulfureus*, Mikan, s. (Sld.); (d) *Syrphidae*: (27) *Pipiza lugubris*, F.; (28) *Cheilosia fraterna*, Mgn.; (29) *Syrphus nitidicollis*, Mgn., f.p.; (30) *Melithreptus tæniatus*, Mgn., f.p.; (31) *Volucella pellucens*, L. (Sld.); (32) *Syritta pipiens*, L., s.; (33) *Eristalis arbustorum*, L.; (34) *E. horticola*, Deg. (Sld.); (35) *E. nemorum*, L.; (36) *E. sepulcralis*, L.; (37) *E. æneus*, Scop., all five species very ab., f.p.; (38) *Helophilus florens*, L., f.p.; (39) *H. pendulus*, L.; (e) *Conopidae*: (40) *Conops flavipes*, L., s.; (41) *Sicus ferrugineus*, L., s.; (f) *Muscidae*: (42) *Echinomyia tessellata*, F.; (43) *Pollenia Vespillo*, F., f.p. and s.; (44) *Lucilia cornicina*, F.; (45) *L. silvarum*, Mgn.; (46) *Pyrellia ænea*,

Zett. ; (47) *Musca corvina*, F. ; (48) *Scatophaga stercoraria*, L., s. ; (49) *Macquartia prætica*, Zett. ; (50) *Sepsis* sp., s. C. Lepidoptera—(a) *Rhopalocera* : (51) *Melitæa Athalia*, Esp. ; (52) *Hesperia alveolus*, H. ; (53) *Satyrus Janira*, L. ; (b) *Sphinges* : (54) *Ino statices*, L., freq. ; (c) *Noctuæ* : (55) *Anarta myrtilli*, L., all s. D. Coleoptera—(a) *Nitidulidæ* : (56) *Meligethes*, very ab. ; (b) *Dermestidæ* : (57) *Anthrenus pimpinellæ*, F., f.p. ; (c) *Elateridæ* : (58) *Athous niger*, L. ; (d) *Lamellicornia* : (59) *Cetonia aurata*, L. (Sld.) ; (60) *Trichius fasciatus*, L., ab. ; (61) *Tr. nobilis*, L. ; (e) *Malacodermata* : (62) *Malachius æneus*, L. ; (63) *Dasytes flavipes*, F. ; (64) *Trichodes apiarius*, L. ; (f) *Mordellidæ* : (65) *Mordella aculeata*, L., ab. ; (66) *M. fasciata*, F. ; (g) *Cerambycidæ* : (67) *Strangalia attenuata*, L. ; (68) *St. armata*, Hbst. ; (69) *St. atra*, F. ; (70) *St. melanura*, L., ab. ; (71) *Leptura livida*, F., very freq. ; (72) *Pachyta octomaculata*, F. (Sld. Siebengebirge). See also No. 590, III., and No. 609.

Altogether I have observed on *C. leucanthemum*—

	Apidæ.	Other Hymenoptera.	Lepidoptera.	Diptera.	Coleoptera.	Hemiptera.	Total.
In Low Germany	14	11	8	30	21	—	84
On the Alps ...	5	2	34	20	6	1	68

In each 100 insect-visitors there are therefore—

	Apidæ.	Other Hymenoptera.	Lepidoptera.	Diptera	Coleoptera.	Hemiptera.	Total.
In Low Germany	16·6	13·1	9·5	35·7	25·0	—	99·9
On the Alps ...	7·4	2·9	50·0	29·4	8·8	1·4	99·9

230. *CHRYSANTHEMUM INODORUM*, L.—The only visitors that I have noticed are *Hedychrum lucidulum*, Dhlb. ♂ (*Chrysidæ*), and *Ulidia erythrophthalma*, Mgn. (*Muscidæ*).

231. *CHRYSANTHEMUM CORYMBOSUM*, L.—(Thuringia):—

Visitors : A. Hymenoptera—*Sphegidæ* : (1) *Cerceris variabilis*, Schrck. ♀. B. Diptera—*Muscidæ* : (2) *Ulidia erythrophthalma*, Mgn. C. Hemiptera—(3) *Capsus* sp., s. Additional visitors (nine Coleoptera, four Diptera, one Hemiptera, five Hymenoptera, three Lepidoptera) are enumerated in No. 590, III.

## 232. CHRYSANTHEMUM PARTHENIUM, Pers :—

Visitors : Lepidoptera—*Sphinxes* : *Sesia tipuliformis*, L., s., also *Halictus* and *Fœnus* (No. 590, III.).

233. MATRICARIA CHAMOMILLA, L.—The general structure of the flower agrees with that of *C. leucanthemum*, but the receptacle of the capitulum is always more convex in this plant.

As the centripetal development of the florets proceeds, the receptacle rises up into a cylinder, rounded off above. Those florets which have ceased blooming always occupy the outer rim around the cylinder, those that are still in the bud occupy its rounded apex, those that are in full bloom occupy the space between on which insects alight. The result of this peculiarity is that insects always come at once to the right spot for obtaining their booty and for fertilising the flowers.

In regard to conspicuousness, *M. Chamomilla* is far inferior to *C. leucanthemum*; for each capitulum forms a white circle 18 to 24 mm. in diameter against 40 mm. or more in *C. leucanthemum*, with a yellow central disk 6 to 8 mm. in diameter against 12 to 15 mm. in the other. Accordingly its insect-visitors are far less numerous and less varied. The strong odour which the capitula emit seems disagreeable to most bees; only the species of *Prosopis*, which are themselves strong-smelling, are fond of the plant, as they are also of *Ruta graveolens*, etc. The odour seems pleasant, on the other hand, to flies; they are found abundantly on the capitula, and constitute the chief fertilisers of the plant.

Visitors : A. Hymenoptera—(a) *Apidæ* : (1) *Prosopis signata*, Pz. ♂ ♀, ab.; (2) *Sphcodes gibbus*, L. ♀ ♂; (b) *Sphégidæ* : (3) *Oxybelus uniglumis*, L., ab. B. Diptera—(a) *Stratiomyidæ* : (4) *Nemotelus pantherinus*, L., very ab., s.; (b) *Empidæ* : (5) *Empis livida*, L., ab., s.; (c) *Syrphidæ* : (6) *Eristalis arbustorum*, L.; (7) *E. nemorum*, L.; (8) *E. sepulcralis*, L., all three very ab., f.p.; (9) *Syritta pipiens*, L., very ab., f.p.; (d) *Muscidæ* : (10) *Sarcophaga carnaria*, L., ab.; (11) *S. hæmorrhœa*, Mgn.; (12) *Pollenia Vespillo*, F., all three f.p.; (13) *Lucilia cornicina*, F.; (14) *Spilogaster nigrita*, Fallen. C. Coleoptera—(a) *Nitidulidæ* : (15) *Meligethes*, ab.; (b) *Cerambycidæ* : (16) *Leptura livida*, L.; (17) *Strangalia attenuata*, L., both not rare. See also No. 590, III.

234. TANACETUM VULGARE, L.—Several hundred florets are united in a flat discoid capitulum, to which radiating marginal florets would be of no use, since numerous capitula stand close together almost forming a single surface. The union of capitula

to form one golden-yellow surface is not only of advantage to this plant by increasing its conspicuousness and thereby attracting more insects, but also, as in *Achillea*, because the insects easily pass without interruption over the whole surface and cross-fertilise very many florets with their feet in the shortest possible time. It is of especial advantage to pollen-collecting bees and pollen-feeding flies, letting them perform their work in the quickest and most convenient manner; and this advantage to the insects reacts upon the plant itself, since these pollen-seeking insects naturally prefer those flowers which offer them such perceptible advantages. The honey is generally accessible, since the throat of the corolla is only 1 mm. deep. The condition of the style aids in the simultaneous fertilisation of many florets by a single visitor. It bears at its apex a capitate tuft of divergent hairs, and in the first stage of the flower it presses the pollen out of the anther-cylinder, raising it just so high that it can be swept off the surface of the capitulum by the insects; afterwards in the second stage, it spreads out its two branches, set with stigmatic papillæ on their inner surfaces, in the same place that the pollen occupied before.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, s.; (2) *Colletes fodiens*, K. ♂ ♀, s. and c.p., very ab.; (3) *C. Daviesiana*, K. ♂ ♀, s. and c.p., still more ab.; (4) *Halictus maculatus*, Sm. ♂ ♀, s. and c.p. very ab.; (5) *Andrena fulvicrus*, K. ♂, s.; (6) *A. denticulata*, K. ♀, c.p.; (7) *Sphecodes gibbus*, L. ♂ ♀, several varieties, including *ephippia*, L., s., and receiving some pollen upon their hairs; (b) *Sphegidae*: (8) *Dinetus pictus*, F. ♀ ♂, freq.; (9) *Mellinus arvensis*, L.; (10) *Crabro* sp.; (c) *Vespidae*: (11) *Odynerus parietum*, L. ♂. B. Diptera—(a) *Stratiomyidae*: (12) *Odontomyia viridula*, F., ab.; (b) *Syrphidae*: (13) *Eristalis arbustorum*, L.; (14) *E. nemorum*, L.; (15) *Syrphus ribesii*, L., all three f.p., ab.; (16) *Syrphid pipiens*, L., s. and f.p., very freq.; (17) *Melithreptus tæniatus*, Mgn., f.p.; (c) *Muscidae*: (18) *Sarcophaga carnaria*, L. C. Lepidoptera—(a) *Rhopalocera*: (19) *Polyommatus Phloas*, L. (as late as Oct. 19); (20) *P. doris*, Hfn.; (21) *Vanessa Atalanta*, L. (as late as Sept. 27); (b) *Noctuae*: (22) *Hadena didyma*, Esp. ♂, s., by day; (c) *Crambina*: (23) *Botys purpuralis*, L., all s. D. Coleoptera—*Coccinellidae*: (24) *Coccinella bipunctata*, L.; (25) *C. quinquepunctata*, L. E. Hemiptera—(26) Several species of bugs. F. Neuroptera—(27) *Panorpa communis*, L., freq. See also No. 590, III.

235. *ARTEMISIA DRACUNCULUS*, L., is anemophilous, but Herr Borgstette has seen it visited by *Melanostoma mellina* (*Syrphidae*).

#### Tribe *Senecionideæ*.

236. *TUSSILAGO FARFARA*, L.—In centre of each capitulum are thirty to forty male florets, around which stand about three hundred

female florets. At night and in dull weather the capitulum closes up, but in sunshine it expands to a golden-yellow disk 20 to 25 mm. in diameter. The central florets have an ovary with an abortive ovule; around the base of the style is a yellow, fleshy nectary, which is visible through the base of the white tube of the corolla, which is 4 mm. long. The honey rises into the dark-yellow, conical throat, which is more than 1 mm. long; from this throat the anther-cylinder protrudes. The branches of the style remain coherent almost to the tip, and are covered above and on their outer sides with short sweeping-hairs. The marginal florets have a perfect ovule, a tube 3 mm. long, devoid of honey, and a narrow linear outer lobe 6 to 8 mm. long. The style projects 2 to 3 mm. beyond the tube of the corolla, and divides into two branches not half a millimetre long, furnished on their inner surfaces with stigmatic papillæ and on their outer surfaces and at their tips with sweeping-hairs which are no longer of use to them. Thus division of labour has here taken place: the marginal florets make the capitulum conspicuous and produce seed, while the central florets secrete honey and produce pollen. The stigmas in the marginal florets are distinctly developed before the pollen emerges at the top of the anther-cylinder; so that if sufficient insect-visits occur, cross-fertilisation of separate capitula always takes place. In absence of insects self-fertilisation is obviously impossible.

Visitors (April 11, 1869, Stromberg Hill): A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, in hundreds, s. and c.p.; (2) *Andrena fulvicrus*, K. ♀, do.; (3) *A. Gwynana*, K. ♀, s. and c.p., freq.; (4) *A. parvula*, K. ♀, do.; (5) *Halictus nitidus*, Schenck, ♀, c.p. B. Diptera—(a) *Bombylidæ*: (6) *Bombylius major*, L., s.; (b) *Syrphidæ*: (7) *Eristalis tenax*, L., f.p. C. Coleoptera—*Nitidulidæ*: (8) *Meligethes*, f.p., freq. A list of Alpine visitors (twenty-one flies, three bees, one ant, two Lepidoptera) is given in my *Alpenblumen* (609).

*Petasites albus*, Gärtner, is dioecious, and, as is usual in dioecious plants, the male capitula are the more conspicuous. In the female capitula there are two kinds of florets. In the centre are some whose only function is to produce honey, but which possess functionless stamens and pistil; and around these stand a much larger number of female florets, which produce no honey and possess no stamens. The male capitula may consist of florets of one kind only; these secrete honey and possess a style, whose branches sweep out the pollen from the anther-cylinder by means of hairs in the ordinary way but are not provided with stigmatic papillæ. But the male capitula, as often as not, contain some small *functionless* florets

also; these occupy the same position in the male capitulum as the sexual florets in the female, and they resemble the latter in the complete absence of a nectary and of stamens, in the possession of a style, and in the very narrow tubular corolla. They are obviously degenerate female florets, which occupy in reduced numbers and in a functionless condition the place that in the primitively hermaphrodite or gynomonœcious capitulum was occupied by functional female florets (609).

*Homogyne alpina*, Cass., is gynomonœcious. The marginal female florets secrete no honey and have lost all traces of stamens, and their corolla is reduced to a short and narrow tube with a more or less insignificant remnant of a ligulate limb. I have seen the plant visited by five Diptera, one humble-bee, and twenty-eight Lepidoptera (609).

### 237. *ARNICA MONTANA*, L. (Sld.) :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. and c.p., ab. ; (2) *Bombus pratorum*, L. ♀, s. ; (3) *Andrena Gwynana*, K. ♀, c.p. B. Diptera—(a) *Bombylidae* : (4) *Anthrax hottentotta*, L. ; (b) *Empidæ* : (5) *Empis tessellata*, F., s., ab. ; (c) *Syrphidae* : (6) *Eristalis horticola*, Mgn. ; (7) *E. arbustorum*, L. ; (8) *E. nemorum*, L., all three very ab., s. ; (9) *Syrphus ribesii*, L., ab. ; (10) *S. umbellatarum*, Mgn. ; (11) *Volucella bombylans*, L., freq. ; (12) *V. pellucens*, L., all s. and f.p. (d) *Conopidae* : (13) *Sicus ferrugineus*, L., s. C. Lepidoptera—*Rhopalocera* : (14) *Argynnis Aglaia*, L. (15) *Vanessa urticae*, L. ; (16) *Vanessa Io*, L., all three s. D. Coleoptera—(a, *Lamellicornia* : (17) *Trichius fasciatus*, L. ; (b) *Chrysomelidae* : (18) *Cryptocephalus sericeus*, L.

The structure of the flower is described in my *Alpenblumen*. On the Alps I have found it visited by three beetles, seven flies, four humble-bees, and thirty-four Lepidoptera.

238. *SENECIO JACOBÆA*, L.—Sixty to eighty florets, each consisting of a tube  $2\frac{1}{2}$  to 3 mm. long and a throat equally long, are united into a disk 7 to 10 mm. in diameter; twelve to fifteen radiating marginal florets increase this diameter threefold. The style has the same characters as in *Tanacetum*.

Visitors : A. Hymenoptera—(a) *Apidæ* : (1) *Apis mellifica*, L. ♀, s. and c.p. ; (2) *Bombus lapidarius*, L. ♀ ♂. c.p. and s. ; (3) *B. pratorum*, L. ♀ ♂, c.p. and s. ; (4) *B. campestris*, Pz. ♂, s. ; (5) *Andrena fulvicrus*, K. ♀, c.p. (6) *A. denticulata*, K. ♀, c.p. ; (7) *Halictus cylindricus*, F. ♂ ; (8) *H. albipes*, F. ♂ ; (9) *H. maculatus*, Sm. ♂ ; (10) *H. nitidus*, Schenck, ♂, all s. ; (11) *Nomada varia*, Pz. ♀, very freq. ; (12) *N. zonata*, Pz. ♀ ; (13) *N. fulva*, Pz. ♀ ; (14) *N. ferruginata*, K. ♀, all s. ; (15) *Osmia spinulosa*, K. ♀, c.p.

(Thuringia) ; (16) *Heriades truncorum*, L. ♀ ♂, s. and c.p. (b) *Tenthredinidæ* : (17) *Tarpa cephalotes*, F. (Thur.) B. Diptera—(a) *Stratiomyidæ* : (18) *Odontomyia viridula*, F., s. and f.p., very ab. ; (b) *Syrphidæ* : (19) *Eristalis tenax*, L. ; (20) *E. nemorum*, L. ; (21) *E. arbustorum*, L. ; (22) *E. sepulcralis*, L. ; (23) *E. æneus*, Scop. ; (24) *Syritta pipiens*, L. ; (25) *Ascia podagrica*, F., all very ab., both s. and f.p. ; (26) *Cheilosia soror*, Zett. ; (27) *Ch. præcox*, Zett. (Teklenburg, Borgst.), freq. ; (c) *Empidæ* : (28) *Empis livida*, L., very a.b., s. ; (d) *Muscidæ* : (29) *Lucilia* sp. ; (30) *Pollenia rudis*, F. ; (31) *Aricia incana*, Wiedem. ; (32) *Onesia floralis*, R. D. ; (33) *O. sepulcralis*, Mgn. ; (34) *Oliviera lateralis*, Pz., very freq. ; (e) *Mycetophilidæ* : (35) *Sciara Thomæ*, L. C. Lepidoptera—(a) *Rhopalocera* : (36) *Polyommatus Phlœas*, L. ; (37) *Satyrus hyperanthus*, L. ; (b) *Sphinges* : (38) *Sesia asiliformis*, Rott. (Thur.), all s. D. Coleoptera : (39) *Edemera virescens*, L., f.p. E. Hemiptera—(40) *Capsus* sp. See also No. 590, III.

239. *SENECIO VULGARIS*, L.—Sixty to eighty florets unite to form a capitulum. In each the tube is  $3\frac{1}{2}$  to 4 mm. long, the throat, to whose base the honey rises, is only 1 to  $1\frac{1}{2}$  mm. long ; the honey is therefore very easily accessible. But since the capitula have no marginal florets with long outer lobes, and are scarcely 4 mm. in diameter, they are very inconspicuous and are very sparingly visited by insects.

In the course of fifteen years I have only seen the plant visited by one drone-fly, *Syritta pipiens*, s. and c.p. freq., and by *Pyrocoris aptera*, L., s. ; Dr. Buddeberg found two bees, *Halictus morio*, F. ♀, c.p., and *Heriades truncorum*, L. ♂, s.

On the other hand, self-fertilisation takes place regularly. The pollen-grains, swept out by the hairs at the tip of the style, remain partly on the edge of the stigmas and partly fall upon their inner surfaces when they separate. It is certain that this self-fertilisation is effectual, for the plant is fully productive even in periods of bad weather, when it is assuredly not visited by insects.

#### Tribe *Cynaroideæ*.

240. *ECHINOPS SPHÆROCEPHALUS*, L.—The corolla is 5 to 6 mm. long and almost filled up by the style ; it is cleft nearly to the base into five linear lobes, and the honey is therefore accessible to very short-lipped insects. The stigmas are not only surrounded by a ring of long hairs at their base, but are covered with short hairs on the whole of their outer surfaces. As the style emerges from the anther-cylinder it sweeps the greater part of the pollen before it but remains dusted with a small part. After emerging, its two branches (stigmas) remain still for some time folded together, so that the insect-visitors may remove the pollen adhering to their

outer surfaces; finally they separate and display their inner surfaces (which are smooth, but capable of fecundation) to the touch of visitors. Self-fertilisation cannot occur.

Hymenoptera—(a) *Apidae*: (1) *Bombus lapidarius*, L. ♀; (2) *B. silvarum*, L. ♀; (3) *B. muscorum*, F. ♀ ♂; (4) *Halictus quadricinctus*, F. ♀ ♂; (5) *H. rubicundus*, Chr. ♂, all s.; (b) *Vespidæ*: (6) *Polistes gallica*, L., and var. *diadema*, ab., s. See also No. 590, III.

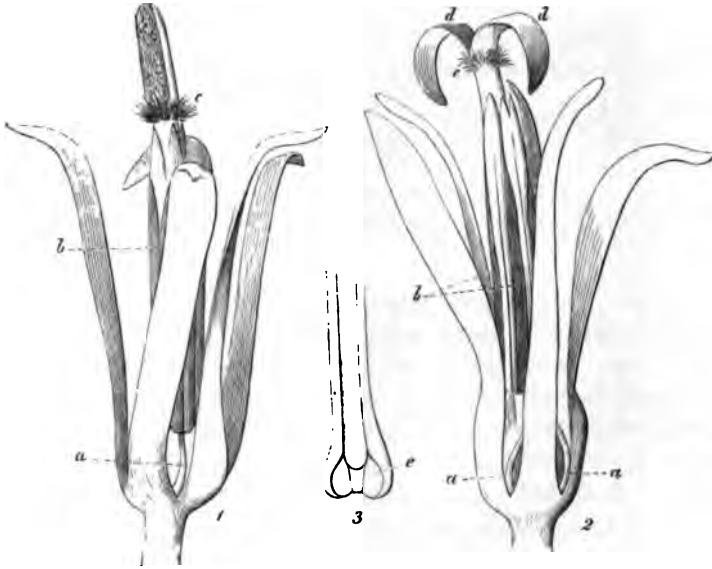


FIG. 118.—*Echinops sphærocephalus*, L.

- 1.—Flower, at close of the first (male) stage.
  - 2.—Ditto, in second (female) stage.
  - 3.—Section of style and corolla-tube around it.
- a, filaments; b, anthers; c, brush on style; d, stigma; e, nectary.

*Echinops Ritro*, L., was found by Delpino to be visited by a sand-wasp, *Scolia bivincta* (178).

241. *CARLINA ACAULIS*, L.—In this plant the involucre bracts play a more important part than usual. The outer ones are armed with such strong spines that, in connection with the spiny leaves, they form a strong safeguard against any attempt to devour the plant. The inner ones help to make the flower conspicuous by day, and at night and in rainy weather close in over the flower to protect it from wet and cold (609).

The opening and closing of the capitulum in *Carlina* and other

Cynareæ is brought about, according to Rathay,<sup>1</sup> by loss and gain of fluid in a layer of sclerenchyma in the involucre bracts.

Visitors in Low Germany: A. Hymenoptera—*Apidae*: (1) *Bombus lapidarius*, L. ♂; (2) *B. confusus*, Schenck, ♂; (3) *B. silvarum*, L. ♂; (4) *B. agrorum*, F. ♂; (5) *B. muscorum*, F. ♂; (6) *B. terrestris*, L. ♂; (7) *B. rupestris*, L. ♂, all very freq., s., sometimes spending the night in the thistle-heads; various males of *Halictus*, the most frequent being (8) *H. cylindricus*, F. ♂, and (9) *H. quadricinctus*, F. ♂. B. Coleoptera—*Curculionidae*: (10) *Larinus senilis*, F. For Alpine visitors, see No. 609.

242. *CARLINA VULGARIS*, L. (Thuringia, end of August and beginning of September 1869):—

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Bombus lapidarius*, L. ♂; (2) *B. terrestris*, L. ♂; (3) *Halictus cylindricus*, F. ♂, very freq.; (4) *H. quadricinctus*, F. ♂; (5) *Megachile circumcincta*, K. ♀; (6) *M. lagopoda*, K. ♂, (only once!); (7) *Cœlioxys quadridentata*, L. ♀; (8) *C. acuminata*, Nyl. ♀; (b) *Sphegidae*: (9) *Ceropales maculata*, F. ♀, all sucking. See also No. 590, III.

243. *ARCTIUM (LAPPA) MINUS*, D.C.—The throat of the corolla is 3 mm. long, with erect, triangular teeth only 1 mm. long; it becomes filled with honey often more than half way up. The branches of the style, which are little over 1 mm. long, are covered over the whole inner surface with colourless stigmatic papillæ, and on the violet outer surface with short, sharp hairs, directed obliquely upwards; these hairs are continued a short distance below the bifurcation of the style and terminate in a ring of longer hairs (cf. Hild. 357, p. 45, pl. v., fig. 32). The style emerges from the anther-cylinder as far as a point 1 to 2 mm. below the ring of longer hairs, and spreads its two stigmatic branches widely apart. Self-fertilisation can scarcely occur.

Visitors: (1) *Bombus agrorum*, L. ♀, s.; (2) *Halictus longulus*, Sm. ♀, s. See also No. 590, III.

244. *ARCTIUM (LAPPA) TOMENTOSUM*, Lam.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, very ab., s. and c.p.; (2) *Bombus agrorum*, F. ♀ ♂, s.; (3) *B. campestris*, Pz. ♂, s.; (4) *B. silvarum*, L. ♀, s.; (5) *Megachile centuncularis*, L. ♀, s. B. Lepidoptera—*Noctue*: (6) *Plusia gamma*, L., s., ab.

245. *CARDUUS CRISPUS*, L.—The expanded throat of the corolla is  $2\frac{1}{2}$  to 3 mm. long, and the linear, very slightly divergent segments

<sup>1</sup> *Sitzungsber. der Akad. der Wissenschaft*, Berlin, vol. lxxxiii, May, 1881.

are 4 to 5½ mm. long. About thirty-five to seventy-eight florets unite in a capitulum, which inferiorly is scarcely 10 mm. in diameter. The tubes of the florets point outwards more and more the nearer they stand to the edge, and the whole capitulum when seen from above appears as a red surface 25 to 30 mm. in diameter. It is also conspicuous when seen from the side. Otherwise the structure of the flowers agrees with that of *Cnicus arvensis*; but the list of insect-visitors is limited by the greater depth of the throat of the corolla.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus agrorum*, F. ♀ ♂, s.; (2) *B. lapidarius*, L. ♀ ♂, s., both ab. (the males as late as October 2); (3) *Halictus cylindricus*, F. ♂, s.; (4) *Osmia fulviventris*, Pz. ♀, c.p.; (5) *Stelis aterrima*, Pz. ♀, s. B. Diptera—*Syrphidæ*: (6) *Eristalis tenax*, L., s. and f.p., ab. C. Lepidoptera—(7) *Pieris napi*, L., s.; (8) *P. rapæ*, L. See also No. 590, III.

246. *CARDUUS ACANTHOIDES*, L.—The capitulum is even more conspicuous than in *C. crispus*, since the narrow segments of the corolla are 7 to 8 mm. long (instead of 4 to 5½). The honey is more easily accessible, for the throat of the corolla is wider than in *C. crispus* and only 2 mm. long (instead of 2½ to 3). Moreover *C. acanthoides* (at Mühlberg, in Thuringia) grows associated in much greater numbers than *C. crispus* (at Lippstadt). These three circumstances account for the very much greater number and variety of insect-visitors in the case of *C. acanthoides*, whose flower has otherwise the same structure as that of *C. crispus*.

A. Hymenoptera—(a) *Apidæ*: (1) *Bombus lapidarius*, L. ♀; (2) *B. silvarum*, L. ♀ ♀; (3) *B. muscorum*, F. ♀; (4) *B. pratorum*, L. ♂; (5) *Dasypoda hirtipes*, F. ♀; (6) *Cilissa tricineta*, K. (*leporina*, Pz.), ♀; (7) *Halictus interruptus*, Pz. ♂; (8) *H. nitidusculus*, K. ♂ ♀; (9) *H. albipes*, F. ♂, ab.; (10) *H. quadricinctus*, F. ♂ ♀, very ab.; (11) *H. rubicundus*, Chr. ♂ ♀, freq.; (12) *H. longulus*, Sm. ♂ ♀; (13) *H. cylindricus*, F. ♂; (14) *H. quadrinotatus*, K. ♂, scarce; (15) *H. maculatus*, Sm. ♂ ♀; (16) *H. minutus*, K. ♂; (17) *H. lucidulus*, Schenck, ♀; (18) *H. Smeathmanellus*, K. ♀, all (1–18) s., only; *H. quadricinctus*, ♀, c.p. also; (19) *H. leucozonius*, K. ♂ ♀, s. and c.p.; (20) *Osmia spinulosa*, K. ♀, very ab., s. and c.p.; (21) *O. aenea*, L. ♂, s.; (22) *O. aurulenta*, Pz. ♀, s. and c.p.; (23) *O. fulviventris*, F. ♀, s. and c.p.; (24) *Megachile lagopoda*, K. ♀ ♂, s. and c.p.; (25) *M. centuncularis*, L. ♂, s.; (26) *M. versicolor*, Sm. ♀, s.; (27) *Chelostoma campanularum*, L. ♀ ♂, s. and c.p.; (28) *Heriades truncorum*, L. ♀ ♂, s. and c. p.; (29) *Stelis phæoptera*, K. ♀, not rare; (30) *St. aterrima*, Pz. ♀ ♂, freq.; (31) *St. breviuscula*, Nyl. ♀; (32) *Prosopis punctulatissima*, Sm. ♀. By far the most important visitors are the bees with abdominal collecting-brushes. I have found *Osmia spinulosa* on *Carduus acanthoides* in the same abundance, and working with the same diligence, as *Megachile* on *Onopordon*. (b) *Vespidæ*: (33) *Cerceris variabilis*, Schr. ♀, s. B. Diptera—(a) *Syrphidæ*: (34) *Eristalis arbustorum*, L., s.;

(b) *Conopidae*: (35) *Conops scutellatus*, Mgn.; (36) *Physocephala rufipes*, F., both s. C. Lepidoptera—(a) *Rhopalocera*: (37) *Pieris brassicæ*, L.; (38) *Argynnis Aglaia*, L.; (b) *Sphinxes*: (39) *Zygæna carniolica*, Scop.; (c) *Noctuæ*: (40) *Plusia gamma*, L., all s. D. Coleoptera—(a) *Elateridæ*: (41) *Corymbites holosericeus*, L.; (b) *Lamellicornia*: (42) *Trichius fasciatus*, L.; (c) *Curculionidæ*: (43) *Larinus Jaceæ*, F.; (d) *Chrysomelidæ*: (44) *Cryptocephalus sericeus*, L. See also No. 590, III.

#### 247. *CARDUUS NUTANS*, L.:—

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus hortorum*, L. ♂; (2) *B. pratorum*, L. ♀ ♂; (3) *B. vestalis*, Fourc. ♂; (4) *Halictus cylindricus*, F. ♂; (5) *H. malachurus*, K. ♀, all s. B. Lepidoptera—*Sphinxes*: (6) *Zygæna loniceræ*, Esp. See also No. 590, III.

*Carduus defloratus*, L.—I have seen this species visited by 103 species of insects, of which fifty-four were Lepidoptera, mostly butterflies (609).

248. *CNICUS (CIRSIUM) ARVENSIS*, L.—Somewhat over a hundred florets are united in one capitulum. The tube of each floret is 8 to 12 mm. long, the wider throat 1 to 1½ mm. long, and the five linear, slightly divergent segments are 4 to 5 mm. long. The capitulum is scarcely 8 mm. in diameter in its lower bracteate portion, but when seen from above it forms a red surface 20 mm. or more in diameter. Since the honey rises up into the throats of the florets, numerous insects of various orders, attracted by the conspicuous capitula, are able to enjoy it. A proboscis need only be 1 to 1½ mm. long to reach to the bottom of the throat of a floret, so that the rich store of honey is accessible not only to bees and Lepidoptera, but also to wasps, flies, and beetles, which seek it diligently. In the first stage of the flower, a large quantity of pollen emerges at the upper end of the anther-cylinder, pressed up by the lengthening style. Owing to their slight stickiness and to the possession of sharp processes over their whole surface (Fig. 114, 2, 3) the pollen-grains adhere easily to one another and to the hairs upon the insect. Gradually the style itself protrudes 2 to 2½ mm. from the anther-cylinder. At its end it divides into two branches nearly 2 mm. long, which are thickly covered on their outer surface with small, sharp hairs (Fig. 114, 5, c). Immediately below the division of the style, this hairy surface ends in a ring of longer hairs (b). On emerging from the anther-cylinder the tip of the style is thickly covered all round with pollen; if sufficient insect-visits occur, (and in fine

weather they never fail) the pollen is in a short time all removed. But if insects do not visit the flower until the stigmatic edges of the branches of the style have already bent outwards, then self-fertilisation is possible, since in this case the hairs of the style still remain covered with pollen. If insects do not visit the flower at all, some of the pollen-grains, which hang in little clumps

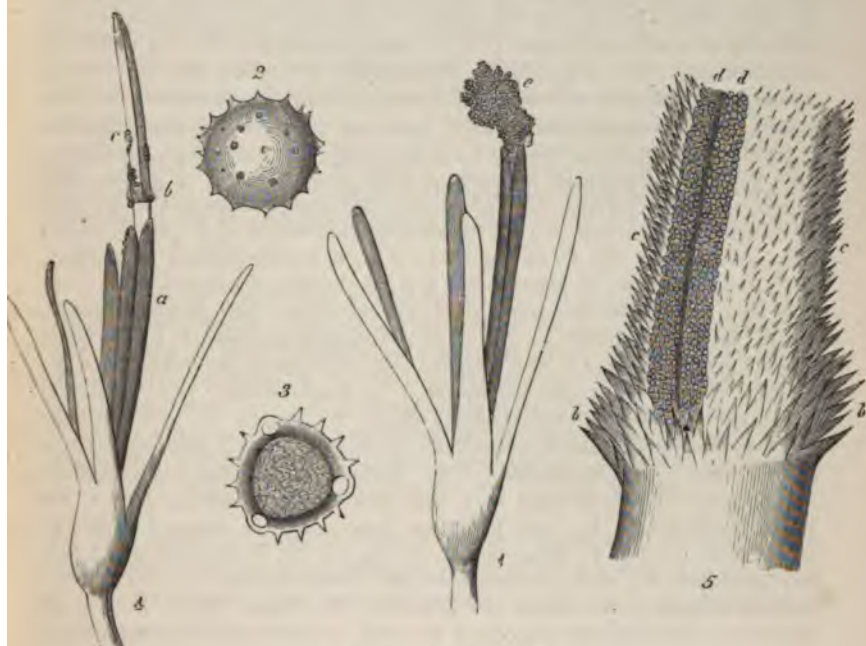


FIG. 114.—*Cnicus arvensis*, L.

- 1.—Flower, in first stage; pollen issuing from the anther-cylinder.
- 2.—Pollen-grain ( $\times 400$ ).
- 3.—Ditto, in optical section.
- 4.—Flower, in second stage. The pollen has been removed by insects and only a few grains remain upon the style; the style projects far beyond the anther-cylinder, and its stigmatic branches are closely applied together.
- 5.—Upper part of style with its ring of long hairs (bb), and lower part of its two stigmatic branches; the latter are covered outside with short hairs, and on the edges with stigmatic papillae ( $\times 88$ ).

a, anther-cylinder; b, ring of long hairs; c, short hairs; d, stigmatic papillae; e, pollen.

to the hairs, may easily fall of themselves upon the stigmatic papillae. In fine weather, and in the open air, this can scarcely ever take place, for *Cnicus arvensis* is one of the most abundantly visited of all our native plants. As the following list shows, very few insects resort to it for the sake of its pollen, but very many for its honey:—

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, in great abundance, some c.p., mostly sucking; (2) *Bombus lapidarius*, L. ♀, s.; (3) *B. hortorum*, L. ♂, s.; (4) *Dasygaster hirtipes*, F. ♀ ♂, c.p. and s., the ♂ numerous; (5) *Cilissa leporina*, Pz. ♂, s., freq.; (6) *Andrena fulvicrus*, K. ♀; (7) *A. dorsata*, K. ♀ ♂, ab.; (8) *A. Gwynana*, K. ♀ ♂, freq.; (9) *A. nana*, K. ♂; (10) *A. pilipes*, F. ♂; (11) *A. vitrea*, Sm. (= *nitens*, Schenck), ♂, Cassel; (12) *Halictus flavipes*, F. ♀; (13) *H. longulus*, Sm. ♂; (14) *H. tarsatus*, Schenck, ♀; (15) *H. nitidiusculus*, K. ♂; (16) *H. minutus*, K. ♀; (17) *H. maculatus*, Sm. ♀; (18) *H. cylindricus*, F. ♀ ♂, very ab.; (19) *H. albipes*, F. ♂; (20) *H. rubicundus*, Chr. ♂; all the species of *Andrena* and *Halictus* and all the following bees only suck honey; (21) *Nomada solidaginis*, Pz. ♀ ♂; (22) *N. Roberjeotiana*, Pz. ♀ ♂; (23) *N. lineola*, Pz. ♀ ♂, ab.; (24) *N. nigrita*, Schenck, ♂; (25) *N. Jacobææ*, Pz. ♀ ♂, ab.; (26) *Epeolus variegatus*, L. ♀ ♂, scarce; (27) *Sphecodes gibbus*, L. ♀ ♂, several varieties, including *ephippia*, L.; (28) *Prosopis communis*, Nyl. ♀, ab.; (29) *P. confusa*, Nyl. (*hyalinata*, Sm.), ♀ ♂; (30) *P. sinuata*, Schenck, ♂; (31) *P. variegata*, F. ♀ ♂, ab.; (32) *Heriades truncorum*, L. ♀; (b) *Sphegidae*: (33) *Crabro cribrarius*, L. ♀; (34) *Cr. alatus*, Pz. ♀ ♂, very ab.; (35) *Lindenius albilabris*, F. ♀ ♂; (36) *Oxybelus trispinosus*, F. ♀; (37) *O. uniglumis*, L. ♀ ♂, ab.; (38) *Cerceris arenaria*, L. ♀ ♂, not rare; (39) *C. nasuta*, Kl. ♀ ♂, ab.; (40) *C. variabilis*, Schr. ♀ ♂, very ab.; (41) *Philanthus triangulum*, F. ♀ ♂, freq.; (42) *Bembex rostrata*, L. ♀; (43) *Dinetus pictus*, F. ♀ ♂; (44) *Ammophila sabulosa*, L.; (45) *Salix sanguinolentus*, F., all s.; (c) *Chrysidæ*: (46) *Hedychrum lucidulum*, Latr. ♀, s.; (d) *Ichneumonidæ*: (47) Various sp.; (e) *Tenthredinidæ*: (48) *Tenthredo notha*, Kl.; (49) Several undetermined sp., s. B. Diptera—(a) *Stratiomyidæ*: (50) *Odontomyia viridula*, F., not rare, s.; (b) *Tabanidæ*: (51) *Tabanus rusticus*, L., s., freq.; (c) *Bombylidæ*: (52) *Anthrax flava*, Mgn. (Thuringia); (d) *Syrphidæ*: (53) *Syrphus* sp.; (54) *Melithreptus tæniatus*, Mgn.; (55) *Eristalis sepulchralis*, L.; (56) *E. æneus*, Scop.; (57) *E. tenax*, L.; (58) *E. arbustorum*, L.; (59) *E. nemorum*, L., all ab., s.; (60) *E. intricarius*, L.; (61) *Syritta pipiens*, L., ab.; (e) *Conopidæ*: (62) *Conops flavipes*, L.; (63) *Physocephala rufipes*, F., s., freq.; (f) *Empidæ*: (64) *Empis livida*, L., s.; (g) *Muscidæ*: (65) *Ocyptera brassicaria*, F.; (66) *O. cylindrica*, F., both freq., s.; (67) *Sarcophaga carnaria*, L., s.; (68) *Onesia floralis*, R. D.; (69) *Lucilia sericata*, Mgn.; (70) *L. cornicina*, F., ab., s.; (71) *Musca corvina*, F., s., ab.; (72) *Oliviera lateralis*, F., s.; (73) *Platystoma seminationis*, F. C. Lepidoptera—(a) *Rhopalocera*: (74) *Vanessa urticae*, L.; (75) *Pieris brassicae*, L., freq.; (76) *Rhodocera rhamni*, L.; (77) *Hesperia silvanus*, Esp.; (78) *Satyrus Janira*, L.; (79) *Thecla rubi*, L.; (b) *Sphingæ*: (80) *Zygaena carniolica*, Scop. (Thuringia), all s.; D. Coleoptera—(a) *Elateridæ*: (81) *Agriotes gallicus*, Lap. (Thur.); (82) *A. ustulatus*, Schaller (Thur.); (b) *Lamellicornia*: (83) *Trichius fasciatus*, L.; (c) *Mordellidæ*: (84) *Mordella fasciata*, L.; (85) *M. aculeata*, L., both freq.; (d) *Malacodermata*: (86) *Telephorus melanurus*, F., very abundant, thrusting their heads into the tube, and also pairing upon the flowers; (e) *Curculionidæ*: (87) *Bruchus*, sp.; (88) *Larinus Jaceæ*, L. (Thur.). See also No. 590, III., for additional visitors in Low Germany. A list of Alpine visitors (four Coleoptera, six Diptera, seven bees, one Sphegidae, and fourteen Lepidoptera) is given in my *Alpenblumen* (No. 609).

## 249. CNICUS (CIRSIUM) OLERACEUS, L.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, s.; (2) *Bombus*, s. B. Lepidoptera—*Noctuæ*: (3) *Euclidia glyphica*, L., s. See also No. 609.

I have not investigated the flowers closely.

250. CNICUS LANCEOLATUS, Scop.—The chief difference between the flowers of this species and of *C. arvensis* is that here the honey is much less accessible. For not only are the narrow tubes of the florets, and accordingly the involucre also, much longer (16 to 18 mm.), which has no effect on the accessibility of the honey; but the throat, in whose base the honey collects, is also much longer (4 to 6 mm. against 1 to 1½ in *C. arvensis*). From this cause the variety of insect-visitors is greatly limited; but the flowers are all the more diligently visited by long-proboscised bees, especially humble-bees.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀; (2) *Bombus terrestris*, L. ♀ ♂; (3) *B. agrorum*, F. ♀ ♂; (4) *B. lapidarius*, L. ♀ ♂ (as late as Oct. 9, 1869!), all four ab., s.; (5) *B. campestris*, Pz. ♂, s.; (6) *Megachile maritima*, K. ♀, c.p.; (b) *Vespidæ*: (7) *Polistes gallica*, L., and var. *diadema*, freq. (s. ?). B. Diptera—*Syrphidæ*: (8) *Eristalis tenax*, L.; (9) *E. arbustorum*, L.; (10) *E. nemorum*, L., all three f.p. and s., very ab. (as late as Oct. 13, 1874). C. Lepidoptera—*Rhopalocera*: (11) *Pieris brassicæ*, L., ab., s.; (12) *Hesperia* sp., s. See also No. 590, III., and No. 609.

251. CNICUS ERIOPHORUS, Scop., is visited very abundantly in Thuringia by *Megachile lagopoda*, K. ♀ ♂, s. and c.p. On the Alps I have found it visited by humble-bees and by various Fritillaries (*Argynnis*) (609).

252. CNICUS OCHROLEUCUS, All., has yellowish-white flowers, and is also visited on the Alps by humble-bees and Lepidoptera (609).

253. CNICUS PALUSTRIS, Scop., stands, in regard to the accessibility of its honey and the variety of its insect-visitors, between *C. lanceolatus* and *C. arvensis*. The throat is 2½ mm. long (in *C. arvensis* 1 to 1½, in *C. lanceolatus* 4 to 6); in all other points the flowers of these three species are alike in structure.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, very freq., s.; (2) *Bombus lapidarius*, L. ♀ ♂, c.p. and s.; (3) *B. pratorum*, L. ♀, s.; (4) *B. vestalis*, Fourc. ♀, s.; (5) *B. Rajellus*, Ill. ♀, s.; (6) *Andrena Coitana*, K. ♀, s.; (7) *A. Gwynana*, K. ♂, s.; (8) *Halictus cylindricus*, F. ♀ ♂,

c.p. and s., very freq.; (9) *Megachile centuncularis*, F. ♂, s.; (b) *Sphegidae*: (10) *Lindeni* *albilabris*, F. B. Diptera—(a) *Syrphidae*: (11) *Eristalis tenax*, L., s. and f.p.; (12) *Volucella bombylans*, L., do.; (13) *Syrphus tricolor*, Fallen, f.p.; (b) *Conopidae*: (14) *Sicus ferrugineus*, L., s. C. Lepidoptera—(a) *Rhopalocera*: (15) *Pieris brassicae*, L.; (16) *P. rapae*, L.; (17) *P. napi*, L.; (18) *Hesperius silvanus*, Esp.; (19) *Satyrus Janira*, L.; (b) *Noctua*: (20) *Plusia gamma*, L., all rather freq., s. D. Coleoptera—(a) *Elateridae*: (21) *Agriotes ustulatus*, Schaller (Sld.); (b) *Cerambycidae*: (22) *Strangalia melanura*, L. (Sld.), ab. See also No. 590, III., and No. 609.

*Cnicus palustris* and *C. arvensis* are gynodioecious according to Darwin (167).

*Cnicus acaulis*, All., is visited by humble-bees and by Lepidoptera (590, 609).

*Cnicus spinosissimus*, Scop.—The tube of the corolla is 8 to 9 mm., the throat 4 to 5 mm. long. The insect-visitors are very numerous and various (609).

254. *CNICUS HETEROPHYLLUS*, All.—Several hundred florets unite to form a capitulum (I have counted 259). The tube is 15 mm., the throat 8 mm. long. I have seen the flower visited by *Bombus mesomelas*, ♀ (18 to 20) (609).

255. *ONOPORDUM ACANTHIUM*, L.—In each floret the honey rises in the tube, which is 10 to 12 mm. long, up to the cylindrical somewhat swollen throat, which is 3 to 4 mm. long, and which divides above into five linear segments, 6 to 8 mm. long; these segments do not diverge, but are continued straight upwards from the throat of the corolla. The length of the tube of the corolla in this plant, and in most other *Cynareæ*, has no influence on the accessibility of the honey, since the latter rises up into the throat; it is due only to the development of the involucre, which gives effectual protection to the buds by completely surrounding them in the form of a deep cup; the long tubes also serve to increase the conspicuousness of the flower, as they bend more and more outwards the nearer they are to the margin. The branches of the style are 3 to 4 mm. long; they seem never to diverge in *Onopordum*, but remain closely appressed. They bear on their outer edges rows of stigmatic papillæ, which in the second (female) stage of the flower turn more outwards and expose themselves to the touch of insect-visitors. One millimetre below its division into two branches, the style bears a ring of short hairs, which point obliquely upwards and are long enough to sweep the anther-cylinder ( $\frac{1}{3}$  mm. wide, 8 to 10 mm. long) clear of pollen.

Although in the first stage this cylinder, coated above with pollen, and in the second the tip of the style, with its two rows of stigmatic papillæ, projects 5 to 7 mm. above the segments of the corolla, many florets are fertilised simultaneously by the bees which visit the flowers, particularly by those with abdominal collecting brushes, which diligently sweep up the pollen upon the surface of the capitulum.

On the southern slopes of Mühlberg and Wandersleber Schlossberg in Thuringia, where I observed *Onopordum*, the two handsomest thistles, *Onopordum Acanthium* and *Cirsium eriophorum*, were fertilised chiefly by the handsomest of the tailor-bees, *Megachile lagopoda*, K. The females fly boisterously on to a thistle-head and brush hurriedly over it, holding the abdomen sometimes so high that one can see from far off the red, hairy coat of its under side, or the blue pollen adhering to it. The mid and hindlegs are actively occupied meanwhile in a backward scratching movement, and the head is sunk among the florets. As a rule the female turns once round upon the capitulum in brushing off its pollen. On leaving one capitulum it flies at once to another, until, being laden with sufficient pollen, it flies off to its nest. The males also sit occasionally sucking honey upon these thistle-heads, but they are much more occupied in pursuing the females.

Delpino's generalisation, based on insufficient observations, that Compositæ whose florets are packed closely together to form a level surface are fertilised by bees with abdominal collecting-brushes, while those whose essential organs are long and widely separate are fertilised by *Halictus*, is shown to be incorrect by this and by many more of my observations.

Visitors (in Thuringia): A. Hymenoptera—(a) *Apidae*: (1) *Megachile lagopoda*, K. ♀ ♂, c.p. and s., in extreme abundance; (2) *Osmia fulviventris*, Pz. ♀ ♂, c.p. and s.; (3) *O. spinulosa*, K. ♀, c.p.: (4) *Cœlixys conoidea*, Ill. ♀, s.; (5) *Stelis aterrima*, Pz. ♀ ♂, s.; (6) *Andrena Schrankella*, N. ♀; (7) *Halictus quadristrigatus*, Latr. ♀, s.; (8) *Saropoda bimaculata*, Pz. ♀, s.; (9) *Bombus lapidarius*, L., ♀, s.; (10) *B. terrestris*, L. ♀, s.; (11) *B. rupestris*, F. ♀, s.; (b) *Sphegidae*: (12) *Psammophila affinis*, K. ♀, s. B. Lepidoptera—(a) *Rhopalocera*: (13) *Vanessa urticæ*, L., s.; (14) *Satyrus Galathea*, L., s.; (b) *Sphinges*: (15) *Macroglossa stellatarum*, L., s. C. Coleoptera—(16) *Coccinella mutabilis*, Scriba, trying vainly to reach the honey. D. Hemiptera—(17) *Capsus*, two species, s. See also No. 590, III., and No. 609.

## 256. SERRATULA TINCTORIA, L. :—

Visitors (at Mühlberg in Thuringia, Sept. 1871): A. Hymenoptera—*Apidae*: (1) *Bombus agrorum*, F. ♀ ♂, s., ab. B. Lepidoptera—*Rhopalocera*: (2) *Colias hyale*, L., s., ab.

In this species there exist female and hermaphrodite plants with a close series of intermediate forms. The seeds of the female flowers are larger than those of the hermaphrodite.<sup>1</sup>

257. *CENTAUREA JACEA*, L.—The capitulum contains as a rule from sixty to over a hundred florets; in these the tubular part of

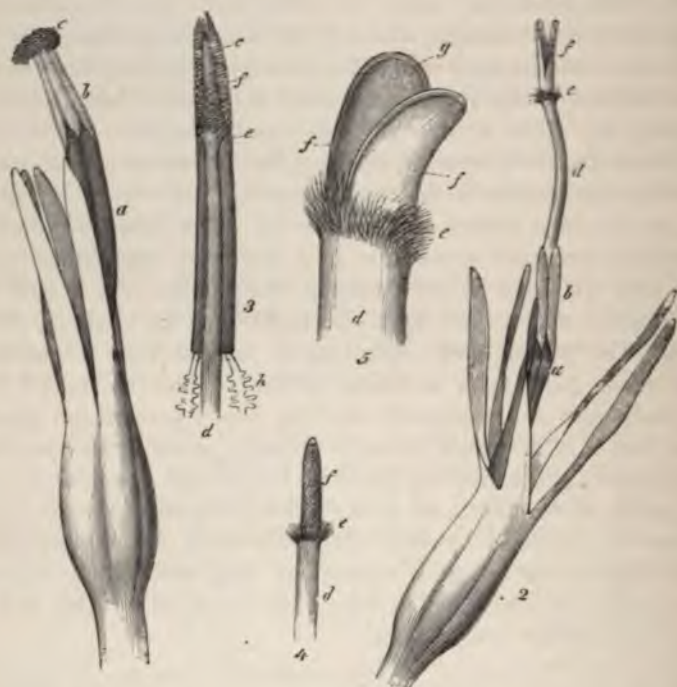


FIG. 115.

1-4.—*Centaurea Jacea*, L.

1.—Upper part of the flower, in first stage ( $\times 7$ ).

2.—Ditto, in second stage.

3.—Section of anther-cylinder, before the pollen has been shed.

4.—End of style, removed from the anther-cylinder, and divested of pollen, to show the fine hairs.

5.—*Centaurea Cyanus*, L. End of style, more magnified.

a, anther-cylinder; b, valvular appendages of the anthers, which at first close the top of the anther-cylinder; c, pollen; d, style; e, ring of sweeping-hairs; f, division of the style; g, stigmatic surface; h, hairs (teeth) upon the filaments, to guard the honey.

the corolla is 7 to 10 mm. long, the expanded bell-shaped part 3 to  $4\frac{1}{2}$  mm. long, and the long, linear segments about 5 mm. long. The capitulum is only 8 to 10 mm. in diameter on a level with the

<sup>1</sup> Sir J. Smith, *Trans. Linn. Soc.* xiii. p. 600, quoted by Darwin, No. 167.

tubular parts of the florets, but since these bend over at their upper ends more and more the nearer they stand to the edge and diverge outwards around the capitulum, a capitulum in full bloom forms a red circular area 20 to 30 mm. in diameter. When a floret opens, its style has the position represented in Fig. 115, 3; its two stigmatic divisions are closely appressed and inclosed in the upper part of the cylinder formed by the coherent anthers; a ring of hairs (Fig. 115, 3, 4, *e*), directed obliquely upwards and touching the inner wall of the anther-cylinder all round, has swept all the pollen into this upper part of the cylinder, so that the branches of the style are closely packed round with pollen. If the flowers in this stage are left untouched for a day or two in a room, the terminal valves of the anther-cylinder separate, and a little pollen appears between them at the top. But if one now touches the filaments with a needle or a sharp pencil (as in a natural condition the insect's proboscis does), a great quantity of pollen is in a short time seen to emerge, and the anther-cylinder is seen to be drawn down so far by the contracting filaments that the branches of the style protrude above. Since their whole outer surface is covered with small hairs directed obliquely upwards, they remain, after emerging from the anther-cylinder, so thickly coated with pollen, that they are not recognisable as branches of the style until the pollen has been brushed away.

Gradually the style grows up still further beyond the anther-cylinder (Fig. 115, 2); the edges (set with stigmatic papillæ) of the inner surfaces of the two branches of the style bend outwards (*g*, 2); and the ends of these branches also gape asunder, so that here also stigmatic papillæ are exposed to the touch of insect-visitors. Spontaneous self-fertilisation can under these circumstances not occur, and self-fertilisation can only be brought about by insects, if, at the time when the stigmatic papillæ become exposed, the outer surfaces of the branches of the style or the ring of hairs are still dusted with pollen; on the other hand, if sufficient insect-visits occur, cross-fertilisation is fully insured. Although the expanded portion of the corolla is longer than in most of our other native Compositæ, and many short-lipped insects (sand-wasps and the majority of flies) are therefore excluded from the honey, yet, in consequence of the great amount of its honey, it is one of the most frequented forms. Various species of bees come in numbers and pay lengthy visits to its capitula, and in creeping between the anther-cylinders and styles protruding from the florets, they bring not only their under-sides, but the greater part of their

hairy bodies in contact at one time with pollen and at another with stigmatic surfaces.

The following insects effect fertilisation:—

A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, ab., s.; (2) *Bombus silvarum*, L. ♀ ♀, s.; (3) *B. agrorum*, F. ♀, s.; (4) *B. pratorum*, L. ♂, s.; (5) *B. rupestris*, F., ♀ ♂, s.; (6) *B. lapidarius*, L. ♀, s.; (7) *B. campestris*, Pz. ♂, s.; all the humble-bees dust chiefly their head, belly, and legs; (8) *Saropoda bimaculata*, Pz. ♀ ♂, very ab.; (9) *Dasygaster hirtipes*, F. ♂, s., freq.; (10) *Andrena pilipes*, F. ♀, c.p.; (11) *Halictus maculatus*, Sm., ♀ ♂, c.p. and s.; (12) *H. quadricinctus*, F. ♀ ♂, c.p. and s., ab.; (13) *H. rubicundus*, Chr. ♀ ♂, c.p. and s.; (14) *H. leucozonius*, K. ♀ ♂, c.p. and s.; (15) *H. interruptus*, Pz. ♂, s.; (16) *H. cylindricus*, F. ♀ ♂, c.p. and s., very ab.; (17) *H. nitidusculus*, K. ♂ ♀, s. and c.p.; (18) *H. albipes*, F. ♂, s.; (19) *H. longulus*, Sm. ♀ ♂; (20) *H. zonulus*, Sm. ♂, s.; (21) *H. minutus*, K. ♂, s.; (22) *H. lucidulus*, Schenck, ♀; (23) *H. Smeathmanellus*, K. ♀, both s. and c.p.; (24) *Nomada succincta*, Pz. ♂, s.; (25) *Osmia spinulosa*, K. ♀, c.p. (Thur.); (26) *Megachile centuncularis*, L. ♀ ♂, s.; (27) *M. lagopoda*, K. ♀, c.p. (Thur.); (28) *Anthidium strigatum*, Latr. ♀, c.p. (Thur.); (b) *Vespidæ*: (29) *Polistes gallica*, F. (Thur.). B. Diptera—(a) *Empidæ*: (30) *Empis rustica*, F., s.; (b) *Syrphidæ*: (31) *Helophilus pendulus*, L., s.; (32) *Eristalis tenax*, L., sometimes c.p., sometimes trying to thrust its rather thick proboscis into the narrow florets; (33) *Rhingia rostrata*, L., s.; (c) *Conopidæ*: (34) *Phytocephala vittata*, F., s.; (35) *Conops flavipes*, L., s. C. Lepidoptera—(a) *Rhopalocera*: (36) *Pieris brassicae*, L.; (37) *P. napi*, L.; (38) *Colias hyale*, L.; (39) *Polyommatus phlaeas*, L.; (40) *Lycæna* sp.; (41) *Satyrus galathea*, L.; (42) *S. megæra*, L.; (43) *S. janira*, L.; (44) *S. pamphilus*, L.; (45) *Hesperia thymas*, Hfn.; (b) *Sphingæ*: (46) *Zygæna lonicerae*, Esp.; (47) *Z. carniolica*, Scop. (Thur.); (c) *Noctuæ*: (48) *Plusia gamma*, L. See also No. 590, III., and No. 609.

I became aware in August, 1881, that the capitula of *Centaurea Jacea* tend to vary along two lines from the commonest and apparently most primitive form which I have just described. The result is, on the one hand, very conspicuous male capitula 50 to 55 mm. in diameter, and on the other hand less conspicuous female capitula 30 to 35 mm. in diameter. In both of these extreme forms the marginal florets have the corolla greatly enlarged, but the reproductive organs functionless. In the male capitula, the florets of the disk possess a style as well as anthers, but its stigmas never separate, but coalesce in their lower part. In the female capitula, the anthers of the disk-florets are brownish, shrunken, and devoid of pollen.

These extreme forms are connected by an unbroken series of transition-stages with the primitive form. As the primitive form began to vary in one direction, the marginal florets became gradually

longer and more radiating, and their reproductive organs diminished *pari passu*, and first the anthers and then the pistil became functionless. Thereupon the marginal florets increased still more in size, the pistils of the disk-florets became functionless, and the male capitula were complete.

Varying in the opposite direction, the corolla in some of the marginal florets got smaller, and gradually the anthers became brown and devoid of pollen; the same changes proceeded step by step towards the centre of the flower, until now we find the whole capitulum consisting only of female florets, and measuring only 15 to 18 mm. in diameter. When this state was reached, the corollæ of the marginal florets began again to increase in size and to radiate outwards, their anthers vanished completely, and their stigmas ceased to unfold.

The capitula on the same plant are always much of the same form. In any locality where capitula of the primitive form occur along with female capitula, *Centaurea Jacea* may be said to be gynodiœcious. But since in the outset of the last described series of changes the outer florets become purely female, before the conspicuousness of the head is visibly diminished, it is clear that my explanation of the origin of gynodiœcism suggested in the cases of *Thymus* and *Glechoma* cannot hold in this instance. It seems much more likely here that the reduced size of the corolla in the female flowers is the result of a tendency to abortion, spreading from the stamens to the corolla. This is Darwin's explanation of all cases of gynodiœcism (No. 167, chap vii. ; 611).

258. *CENTAUREA SCABIOSA*, L., agrees in the whole structure of its flower with the previous species, but differs only in its honey being more easily accessible. For while the tubular parts of the disk-florets are longer than in the previous species (11 to 12 mm.), the expanded part above, which becomes filled with honey, is shorter ( $3\frac{1}{2}$  to 4 mm.), and while in the primitive form of *C. Jacea* the marginal florets and the disk-florets were alike, I have always found in *C. Scabiosa* the marginal florets devoid of stamens and style, devoid of a wide superior portion (or throat), but notably larger (16 to 22 mm. long), with their tubes entirely directed outwards and dividing into five linear segments, differing little from one another and about 2 mm. longer than those of the disk-florets.

The less variety of visitors that I have observed is simply due to the fact that I have only watched this species on a few occasions

(in Thuringia), while I have met with *C. Jacea* in most of my excursions in summer.

Visitors (in Thuringia): A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s., ab.; (2) *Bombus lapidarius*, L. ♂; (3) *B. terrestris*, L. ♂; (4) *B. muscorum*, F. ♀ ♂, c.p. and s.; (5) *B. agrorum*, F. ♂; (6) *B. silvarum*, L. ♂; (7) *B. confusus*, Schenck, ♂; (8) *B. rupestris*, F. ♂; (9) *Halictus quadricinctus*, F. ♀ ♂, very ab., all s.; (10) *H. maculatus*, Sm. ♀, c.p.; (11) *Megachile ligniseca*, K. ♂; (12) *Osmia aenea*, L. ♂, s.; (13) *O. spinulosa*, K. ♀, c.p.; (14) *Anthidium manicatum*, L. ♂, s. B. Diptera—(a) *Syrphidae*: (15) *Eristalis nemorum*, L.; (b) *Muscidae*: (16) *Trypeta cornuta*, F. C. Lepidoptera—(a) *Rhopalocera*: (17) *Satyrus Janira*, L.; (18) *Melitæa Athalia*, Esp.; (b) *Sphinges*: (19) *Zygæna carniolica*, Scop. D. Coleoptera—*Chrysomelidae*: (20) *Cryptocephalus sericeus*, L. E. Hemiptera—(21) *Capsus* sp., s. See also No. 590, III. Thirty-eight Alpine visitors (two Coleoptera, two Diptera, twelve Apidae, twenty-two Lepidoptera) are given in my *Alpenblumen* (No. 609).

259. *CENTAUREA CYANUS*, L. (Fig. 115, 5).—In this species also, the marginal florets serve only to attract insects, but they do so in a more effectual way than in *C. Scabiosa*, for they are large and infundibuliform and radiate outwards, extending the blue surface of the capitulum from 20 to 50 mm. in diameter, and making it also conspicuous in side view. The honey is more easily accessible, for above the narrow tubular part of the floret, which is 5 to 6 mm. long, the wider part is only 3 mm. long to the place where it divides into linear segments. In this species the simultaneous fertilisation of numerous florets goes on to a very slight extent; for the florets of the disk are not numerous, and their anther-cylinders project at wide intervals. I have never seen the irritability of the stamens more distinctly shown in any other Composite. In flowers which I had allowed to develop in my room until the superior valvular appendages of the anthers had separated of themselves, the filaments contracted when I touched them so much that the anther-cylinder was drawn down to an extent of 2 to 3 mm. very quickly, and then more slowly to an extent of 5 to 6 mm.; in a few seconds a mass of pollen emerged from the superior orifice of the anther-cylinder, and then gradually the style protruded 3 to 4 mm. above the same orifice. In the natural condition, I never succeeded in obtaining such distinct action on touching the filaments, doubtless because the filaments had almost always been touched by insects before they had reached the full amount of tension.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, ab., s. and c.p.; (2) *Bombus silvarum*, L. ♀, s.; (3) *Megachile maritima*, K. ♂, s.;

(b) *Sphegidae*: (4) *Psammophila affinis*, K., s. (proboscis 5 mm. long). B. Diptera—(a) *Empidæ*: (5) *Empis livida*, L., s., ab.; (b) *Syrphidæ*: (6) *Eristalis arbustorum*, L., f.p.; (7) *Rhingia rostrata*, L., s. C. Lepidoptera—*Noctuæ*: (8) *Plusia gamma*, L., s. See also No 590, III.

#### Tribe *Mutisiaceæ*.

*Chuquiraga insignis*, R. Br.—The long, tubular florets of this Composite, which grows on the summits of the Andes (Pichincha), are visited, according to Professor Jameson, by a humming-bird (*Oreotrochilus Pichinchæ*). (Delpino, No. 185.)

The cleistogamic flowers of *Anandria* were known to Linnæus (H. von Mohl, No. 531).

#### Tribe *Cichoriaceæ*.

260. *CICHORIUM INTYBUS*, L.—The capitula are closed in rainy weather, but expand in sunshine to form blue disks 30 mm. and upwards in diameter. Each floret has a tube 3 mm. long and a limb 13 mm. long, and this immense development of the limb compensates for the small number of florets in each capitulum. The structure of the florets agrees with that in *Leontodon* and *Hieracium*, except that the branches of the style are much more curved, each making one to two spiral turns; self-fertilisation in absence of insects is thus much more easily effected.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, s., ab.; (2) *Andrena fulvicrus*, K. ♀, c.p.; (3) *Halictus quadricinctus*, F. ♂; (4) *Nitidiusculus*, K. ♂; (5) *H. rubicundus*, Chr. ♂; (6) *H. longulus*, Sm. ♀; (7) *H. albipes*, F. ♂, all s.; (8) *Osmia spinulosa*, K. ♀, s. and c.p. (Thur.), not rare. B. Diptera—(a) *Syrphidæ*: (9) *Syritta pipiens*, L.; (10) *Eristalis tenax*, L., both species s. and c.p.; (b) *Conopidæ*: (11) *Sicus ferrugineus*, L., s. C. Lepidoptera—*Rhopalocera*: (12) *Colias hyale*, L., s. (Thur.). D. Coleoptera—*Malacodermata*: (13) *Malachius bipustulatus*, F., f.p., ab. An additional list of nine bees is given in No. 590, III.

*Hyoseris radiata*, L., is visited by *Megachile centuncularis* (Delpino, No. 178, p. 125).

261. *LAPSANA COMMUNIS*, L.—The capitulum consists of eight to seventeen florets, and expands to a yellow disk 8 to 10 mm. in diameter. In each floret the tube is  $1\frac{1}{2}$  to  $2\frac{1}{2}$  mm. long, and the limb 4 to 6 mm. long. The capitula are solitary and comparatively small; they are therefore not very conspicuous, and insect-visits are very few. In absence of insects, self-fertilisation takes place regularly, and it is doubtless effective, since the capitula are without

exception fertile. The anther-cylinder protrudes 2 to 3 mm. from the tube, and the style  $1\frac{1}{2}$  to 2 mm. beyond the anther-cylinder. The outer surface of the projecting portion of the style is covered with pointed hairs at wide intervals. The stigmatic branches are only  $\frac{1}{2}$  mm. long, and are closely set with papillæ on their inner surfaces; they separate widely, and bring their papillæ regularly in contact with the pollen if insect-visitors have not removed it from the hairs.

Visitors: Diptera—*Syrphidæ*: (1) *Eristalis arbustorum*, L.; (2) *E. nemorum*, L.; (3) *E. sepulcralis*, L., all three species f.p., not abundant. See also No. 590, III.

262. *PICRIS HIERACIOIDES*, L.—The capitulum is composed of forty-four to seventy-five florets, which increase in size from the centre towards the circumference; it expands in sunshine to form a yellow disk 24 to 36 mm. in diameter, in dull weather it closes up till its diameter is scarcely 7 mm. In each floret the tube is 4 to 6 mm. long, and the limb 8 to 12 mm. long. The stem is branched, and nearly three feet high; it bears numerous capitula, so that the whole plant is very conspicuous. The honey rises into the upper and wider part of the tube, and is therefore accessible to very short-lipped insects. The anther-cylinder projects 5 mm. beyond the tube, and the style  $2\frac{1}{2}$  to  $3\frac{1}{2}$  mm. beyond the anther-cylinder; so that most insect-visitors creep rather among than over the styles, and convey the pollen rather with the hairs on their sides than with those on their under surfaces; but bees with abdominal collecting apparatus are also found upon the flowers.

The sweeping-hairs and the stigmatic papillæ are distributed as in the other Cichoriaceæ (cf. Figs. 116, 117). The stigmatic branches usually spread apart as in other cases, but in several instances I have seen the left bent over towards the right, and the right towards the left, so close together that the stigmatic papillæ of the one were brushed by the pollen-holding hairs of the other.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Panurgus calcaratus*, Scop. ♀ ♂, c.p. and s., ab.; (2) *Rhophites* (*Dufourea*) *vulgaris*, Schenck, ♀, ab., ♂, scarce, s. and c.p. (Thur. Wald); (3) *Halictus zonulus*, Sm. ♀; (4) *H. leucozonius*, Schr. ♀; (5) *H. sexnotatus*, K. ♀ ♂; (6) *H. maculatus*, Sm. ♀; (7) *H. cylindricus*, F., ♂; (8) *H. quadricinctus*, F. ♂; (9) *H. rubicundus*, Chr. ♂; (10) *H. nitidiusculus*, K. ♂; (11) *H. albipes*, F. ♂; (12) *H. longulus*, Sm. ♀ ♂; (13) *H. minutus*, K. ♀ ♂; (14) *H. Smeathmanellus*, K. ♀, most of these species in great numbers, the ♂ s., the ♀ c.p. and s.; (15) *Heriades truncorum*, L. ♀, c.p.; (16) *Osmia spinulosa*, K. ♀, c.p. (Thur.); (b) *Sphegidæ*: (17) *Crabro sexcinctus*, v. d. L. ♀. B. Diptera—(a) *Empidæ*: (18) *Empis*

livida, L., very ab., s.; (b) *Syrphidæ*: (19) *Eristalis tenax*, L.; (20) *E. arbustorum*, L.; (21) *E. nemorum*, L.; (22) *E. sepulchralis*, L., all four species very ab.; (23) *Syrphus balteatus*, Deg.; (24) *Melithreptus scriptus*, L.; (25) *M. tæniatus*, Mgn.; (26) *Chrysogaster viduata*, L., all both f.p. and s. C. Lepidoptera—*Rhopalocera*: (27) *Pieris brassicæ*, L.; (28) *P. rapæ*, L., both species very ab.; (29) *Satyrus Janira*, L., all three species s. See also No. 590, III.

#### 263. CREPIS BIENNIS, L.:—

Visitors: A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L., ♀, s.; (2) *Panurgus calcaratus*, Scop., ♀ ♂, c.p., s., very ab.; (3) *P. Banksianus*, K. ♀ ♂, c.p., s., scarcer; (4) *Dasypoda hirtipes*, F. ♂, ab., even in the evening; (5) *Rhophites* (*Dufourea*) *vulgaris*, Schenck, ♀ ♂, very freq. (Thur., Wald.); (6) *Andrena dorsata*, K. ♀, c.p.; (7) *A. denticulata*, K. ♀ ♂, c.p. and s. (Tekl., Borgst.; Thur.); (8) *A. fulvago*, Chr. ♀, c.p. (Thur.); (9) *A. fulvescens*, Sm. ♀, c.p. (Thur.); (10) *A. parvula*, K. ♂, s.; (11) *Halictus longulus*, Sm. ♀; (12) *H. maculatus*, Sm. ♀; (13) *H. leucozonius*, Schr. ♀ ♂, freq.; (14) *H. cylindricus*, F. ♀ ♂, ab.; (15) *H. albipes*, F. ♀; (16) *H. lugubris*, K. ♂; (17) *H. flavipes*, K. ♂; (18) *H. nitidus*, Schenck, ♀; (19) *H. rubicundus*, Chr. ♂; (20) *H. quadricinctus*, F. ♂, ab.; the ♂ of *Halictus* s., the ♀ c.p. and s.; (21) *Osmia spinulosa*, K. ♀, s. and c.p., very ab. (Thur.); (22) *Chelostoma campanularum*, K. ♀ ♂, s. and c.p., very ab.; (23) *Heriades truncorum*, L. ♀ ♂, s. and c.p., very ab. B. Diptera—*Syrphidæ*: (24) *Eristalis tenax*, L.; (25) *E. nemorum*, L.; (26) *E. arbustorum*, L.; (27) *E. sepulchralis*, L.; (28) *Syrpita pipiens*, L., all five species s. and f.p., very ab.; (29) *Syrphus* sp., f.p.; (30) *Cheilosia chrysocoma*, Mgn., f.p. C. Coleoptera—*Nitidulidæ*: (31) *Meligethes*, ab. See also No. 590, III.

#### 264. CREPIS TECTORUM, L.:—

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Rhophites* (*Dufourea*) *vulgaris*, Schenck, ♀ ♂, c.p. and s.; (2) *Andrena denticulata*, K. ♀ ♂ (Tekl., Borgst.); (3) *A. fulvicrus*, K. ♀, c.p.; (4) *Halictus villosulus*, K. ♀, c.p.; (5) *H. rubicundus*, Chr. ♂, s.; (6) *H. quadricinctus*, F. ♂, ab.; (7) *Osmia spinulosa*, K. ♀, c.p., ab. (Thur.); (8) *Heriades truncorum*, L. ♂, s.; (b) *Sphegidæ*: (9) *Pompilus viaticus*, L. ♀, s. B. Diptera—*Syrphidæ*: (10) *Cheilosia chrysocoma*, Mgn., f.p. (Teklenburg, Herr Borgstette). See also No. 590, III.

#### 265. CREPIS VIRENS, Vill.:—

Visitors: A. Hymenoptera—*Apidæ*: (1) *Panurgus calcaratus*, Scop. ♀ ♂, c.p. and s., ab.; (2) *P. Banksianus*, ♀ ♂, scarcer; (3) *Rhophites* (*Dufourea*) *vulgaris*, Schenck, ♀ ♂, c.p. and s., ab.; (4) *Dasypoda hirtipes*, F. ♂, s.; (5) *Andrena denticulata*, K. ♀, c.p. (Thur.; Tekl., Borgst.); (6) *A. dorsata*, K. ♂, s.; (7) *Halictus villosulus*, K. ♀, c.p.; (8) *H. cylindricus*, F. ♀, c.p.; (9) *H. minutus*, K. ♀, c.p. B. Diptera—(a) *Syrphidæ*: (10) *Eristalis tenax*, L. f.p.; (11) *Melithreptus scriptus*, L. f.p.; (12) *M. tæniatus*, Mgn., f.p.; (13) *Syrphus balteatus*, Deg.; (14) *S. ribesii*, L.; (15) *S. arcuatus*, Fallen, all three f.p.; (16) *Cheilosia chrysocoma*, Mgn., f.p. (Tekl. B.); (b) *Conopidæ*: (17) *Sicus ferrugineus*, L., s. C. Coleoptera—*Mordellidæ*: (18) *Mordella fasciata*, F. See also No. 590, III.

266. *HIERACIUM UMBELLATUM*, L.—The florets have a tube 3 to 5 mm., and an outer limb 8 to 16 mm. long, both increasing in length gradually from the centre to the periphery of the capitulum. The whole capitulum, when fully expanded, forms a yellow disk about 25 mm. in diameter.

Honey is secreted by a ring round the base of the style, and rises several millimetres in the tube; a proboscis 2 to 3 mm. long

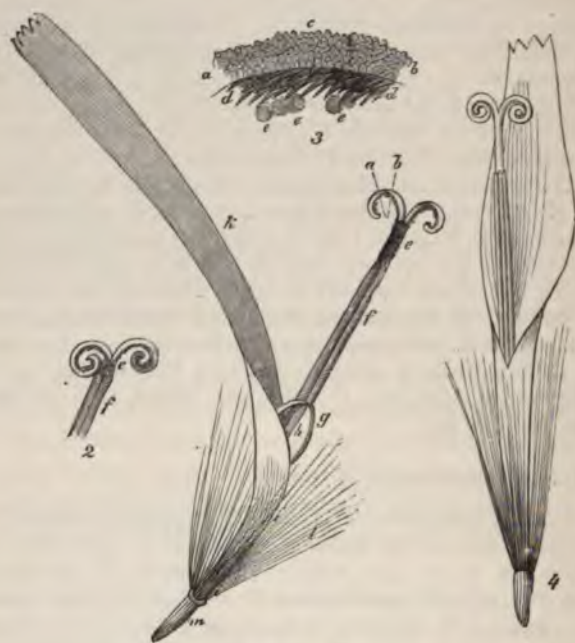


FIG. 116.

1-3 — *Hieracium umbellatum*, L.

1.—Floret, in second stage ( $\times 7$ ).

2.—The stigmas, still more revolute, so that self-fertilisation takes place if the pollen has not all been removed from the hairs.

3.—The portion a—b, of 1 ( $\times 60$ ).

4. *H. pilosella*, L. Floret in the act of self-fertilisation ( $\times 7$ ).

a, stigmatic papillae; b, sweeping hairs; c, pollen-grains; d, anther-cylinder; e, stamens; f, style; g, tube of corolla; h, limb of corolla; i, pappus; m, ovary.

suffices to reach it. Not only the two branches of the style (which are  $2\frac{1}{2}$  mm. long) protrude from the anther-cylinder, but also about  $3\frac{1}{2}$  mm. of the style below its bifurcation; pollen remains adhering to the sharp, bristly hairs (3, d) with which the whole of the projecting part of the style is clothed. After emerging from the anther-cylinder, the two branches of the style, which are

covered all over their inner surface with stigmatic papillæ, spread apart, and gradually bend so far backwards that part of their stigmatic surface comes in contact with the hairs (Fig. 116, 2). So if the pollen has not been removed by insects, self-fertilisation takes place. If insect-visitors come in proper time self-fertilisation is not impossible, but the chances are immensely in favour of cross-fertilisation, and of cross-fertilisation with pollen from other capitula, as the insect on alighting comes at once in contact with the upper surface of the stigmas.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, s. and c.p., ab.; (2) *Bombus lapidarius*, L. ♀, s.; (3) *Dasygaster hirtipes*, F. ♀, s. and c.p.; (4) *Panurgus calcaratus*, Scop. ♀ ♂, s. and c.p., very ab.; (5) *Halictus leuczonius*, Schr. ♀ ♂, s. and c.p.; (6) *H. villosulus*, K. ♀ ♂, s. and c.p.; (7) *Megachile argentata*, F. ♀, s.; (8) *M. Willughbiella*, K. ♂, s.; (9) *Cœlixys conoidea*, Ill. ♀, s.; (10) *C. simplex*, Nyl. ♀, s.; (b) *Chrysidæ*: (11) *Hedychrum lucidulum*, Latr. ♂. B. Diptera—(a) *Syrphidæ*: (12) *Eristalis tenax*, L. (as late as Oct. 13); (13) *E. arbustorum*, L.; (14) *Syrphus balteatus*, Deg., all three species f.p. and s., very ab.; (b) *Conopidæ*: (15) *Sicus ferrugineus*, L., s.; (16) *Occemyia atra*, F., s. C. Lepidoptera—*Rhopalocera*: (17) *Pieris napi*, L., ab.; (18) *Satyrus Megæra*, L.; (19) *Vanessa urticae*, L., not rare; (20) *Hesperia* sp., all s. See also No. 590, III.

267. *HIERACIUM PILOSELLA*, L.—Forty-two to sixty-four florets unite to form a capitulum, and increase in size from its centre to its circumference. In each the tube is 3 to 6 mm. long, and the limb 4 to 8 mm. long. In sunny weather the capitulum expands to form a yellow surface 20 mm. in diameter, but in dull weather it closes up. On the bare slopes where the plant grows abundantly, its capitula are conspicuous enough to attract numerous insects in spite of the small size of the plant.

But on the whole, insect-visits are less abundant, though not less various, than in the previous species, and accordingly, while the flowers are in other respects similar, self-fertilisation is better provided for by the greater involution of the stigmas (Fig. 116, 4).

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Panurgus calcaratus*, Scop. ♀ ♂, c.p. and s., ab.; (2) *Andrena fulvescens*, Sm. ♀; (3) *A. fulvago*, Chr. ♀; (4) *Halictus leuczonius*, Schr. ♀; (5) *H. villosulus*, K. ♀; (6) *H. nitidus*, Schenck, ♀, all c.p., the two *Andrenæ* also s.; (7) *Ceratina cœrulea*, Villa, ♂, s., scarce; (8) *Diphysis serratulæ*, Pz. ♂, s., scarce; (9) *Nomada Fabriciana*, L. ♀, s.; (b) *Tenthredinidæ*: (10) *Cephus*, a small sp. B. Diptera—(a) *Bombylidæ*: (11) *Bombylius canescens*, Mik. (Sld.), s.; (b) *Syrphidæ*: (12) *Helophilus florens*, L., f.p. C. Lepidoptera—(a) *Rhopalocera*: (13) *Pieris brassicae*, L.; (14) *Lycæna argiolus*, L.; (b) *Noctuæ*: (15) *Euclidia* Mi, L., all s. D. Coleoptera—(a) *Cerambycidæ*: (16) *Leptura livida*, L.; (b) *Chrysomelidæ*: (17)

*Cryptocephalus Moræi*, L., ab. ; (18) *C. sericeus*, L., ab. See also No. 590, III., for a further list of visitors in Low Germany. A list of Alpine visitors (four beetles, five flies, five bees, twenty-seven Lepidoptera) is given in my *Alpenblumen* (690).

#### 268. *HIERACIUM VULGATUM*, L. :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Bombus Rajellus*, Ill. ♀, s. ; (2) *B. terrestris*, L. ♀, s. ; (3) *B. silvarum*, L. ♀, s. ; (4) *Andrena Coitana*, K. ♂, s. ; (5) *A. fulvescens*, Sm. ♀, c.p. ; (6) *A. denticulata*, K. ♂, s. ; (7) *Halictus cylindricus*, F. ♀ ♂, c.p. and s., ab. ; (8) *Panurgus calcaratus*, Scop. ♀ ♂, c.p. and s., ab. B. Lepidoptera—*Rhopalocera* : (9) *Lycæna icarus*, Rott., s. See also No. 590, III.

#### 269. *HYPOCHÆRIS GLABRA*, L. :—

Visitors : Hymenoptera—*Apidæ* : (1) *Rhopites* (Dufourea) *vulgaris*, Schenck, ♀, c.p. and s. ; (2) *Andrena fulvescens*, Sm. ♀, c.p. ; (3) *Halictus nitidiusculus*, K. ♀ (Tekl., Borgst.) ; (4) *H. cylindricus*, F. ♀, c.p. ; (5) *Sphecodes gibbus*, L. ♀ ♂, s.

#### 270. *HYPOCHÆRIS RADICATA*, L. :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, c.p. ; (2) *Bombus lapidarius*, L. ♀, s. ; (3) *Dasypoda hirtipes*, F. ♀, c.p., ab. ; (4) *Panurgus calcaratus*, Scop. ♀ ♂, s. and c.p., ab. ; (5) *P. Banksianus*, K. ♀ ♂, s. and c.p., scarcer ; (6) *Colletes Daviesiana*, K. ♀ ♂, c.p. and s., ab. ; (7) *Rhopites* (Dufourea) *vulgaris*, Schenck, ♀, c.p. and s. ; (8) *Andrena xanthura*, K. ♀, s. ; (9) *A. denticulata*, K. ♀ ♂, c.p. and s. (Tekl., Borgst. ; Thur.) ; (10) *A. fulvescens*, Sm. ♀, c.p. (Thur.) ; (11) *A. fulvago*, Chr. ♀, c.p. (Thur.) ; (12) *Halictus villosulus*, K. ♀, c.p. ; (13) *H. malachurus*, K. ♀, c.p. ; (14) *H. lugubris*, K. ♂ ; (15) *H. flavipes*, F. ♂ ; (16) *H. leucozonius*, Schr. ♀ ♂, c.p. and s. ; (17) *H. cylindricus*, F. ♀ ♂, c.p. and s. ; (18) *H. rubicundus*, Chr. ♀, c.p. ; (19) *H. sexstrigatus*, Schenck, ♀, c.p. ; (20) *H. brevicornis*, Schenck, ♂, s. ; (21) *Sphecodes gibbus*, L. ♀ ♂ ; (22) *Diphysis serratulæ*, Pz. ♂, s. B. Diptera—(a) *Syrphidæ* : (23) *Eristalis arbustorum*, L. ; (24) *E. nemorum*, L. ; (25) *E. sepulchralis*, L., f.p. ; (26) *Pipiza funebris*, Mgn., f.p. ; (b) *Conopidæ* : (27) *Sicus ferrugineus*, L., s. ; (c) *Muscidæ* : (28) *Demoticus plebeius*, Fallen, s. See also No. 590, III. and No. 609.

271. *LEONTODON AUTUMNALIS*, L.—The capitulum consists of forty to seventy florets ; it expands in sunshine to a diameter of 20 to 30 mm., and closes up in rainy weather till its diameter is scarcely 5 mm. In each floret the tube is  $2\frac{1}{2}$  to 5 mm. long, and the limb 7 to 12 mm. long. The honey rises up into the wider part of the tube. The anther-cylinder projects 4 to 5 mm. from the tube, the style 3 to 4 mm. beyond the anther-cylinder. The style is covered on its outer surface with pointed sweeping-hairs, and is closely set

with stigmatic papillæ on the inner surface of its branches, which for the most part do not become entirely separated (Fig. 117, 2).

Here, as in *Picris hieracioides*, insect-visitors come in contact with the pollen and stigmas more with their sides than with their under surfaces. Simultaneous fertilisation of numerous florets takes place



FIG. 117.—*Leontodon autumnalis*, L.

1.—Floret, in second (female) stage, after removal of ovary and pappus ( $\times 7$ ).

2.—End of the style in preceding figure ( $\times 35$ ). a, hairs; b, stigmatic papillæ; c, pollen-grains.

here, as in most Cichoriaceæ, to a less extent than in those Senecionidæ and Asteroideæ in which the out-pressed pollen and afterwards the stigmas lie in one plane. In this species, on the other hand, the florets are able at one and the same time to receive pollen from insects upon their stigmas, and to contribute their own to the insect in turn.

If sufficient insects visit the flower in time to remove the pollen from the sweeping-hairs before the stigmatic surfaces appear, cross-fertilisation is alone possible. If insect-visitors only come when the branches of the style have begun to separate, then the possibility of self-fertilisation by insect agency is not excluded. Even in absence of insects, self-fertilisation seems to be not impossible, since when the stigmas separate their edges curve outwards, and their papillæ may easily come in contact with pollen still upon the hairs.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, s.; (2) *Bombus lapidarius*, L. ♀, s.; (3) *Dasypoda hirtipes*, F. ♀, scrambling very rapidly over the capitulum, sucking a few florets, and then flying away to another (the enormously long hairs of the hindlegs carry huge balls of yellow pollen); (4) *Panurgus calcaratus*, Scop., s. and c.p.; (5) *Andrena fulvicrus*, K. ♀, c.p.; (6) *Halictus leucozonius*, Schr. ♀, s. and c.p.; (7) *H. leucopus*, K. ♀; (8) *H. longulus*, Sm. ♀, both species c.p. and s.; (9) *H. Smeathmanellus*, K. ♂; (10) *H. morio*, F. ♂; (11) *H. maculatus*, Sm. ♂; (12) *H. cylindricus*, F. ♂, 9—12 s.; (13) *Diphysis serratulæ*, Pz. ♀ ♂, scarce, s.; (14) *Prosopis armillata*, Nyl. ♂, s.; (b) *Sphegida*: (15) *Pompilus viaticus*, L., s. B. Diptera—(a) *Syrphidæ*: (16) *Syrphus pyrastris*, L., ab.; (17) *S. balteatus*, Deg.; (18) *S. nitidicollis*, Mgn.; (19) *Melithreptus tæniatus*, Mgn.; (20) *Volucella bombylans*, L.; (21) *Eristalis sepulcralis*, L., ab.; (22) *E. arbustorum*, L., very ab. (as late as Oct. 13); (23) *E. tenax*, L., ab., all both f.p. and s.; (b) *Conopidæ*: (24) *Sicus ferrugineus*, L., s. (c) *Bombylidæ*: (25) *Systoechus sulfureus*, F., s.; (d) *Muscidæ*: (26) *Sarcophaga carnaria*, L., s. only. C. Lepidoptera—(a) *Rhopalocera*: (27) *Colias hyale*, L. (Thur.) s.; (b) *Noctuæ*: (28) *Plusia gamma*, L. (as late as Oct. 14), s. See also No. 590, III.

## 272. LEONTODON HASTILIS, L. (Koch):—

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Bombus Barbutellus*, K. ♀, s.; (2) *B. pratorum*, L. ♀, s. and c.p.; (3) *Andrena fulvescens*, Sm. ♀, s. and c.p., dusting itself very thickly with pollen (Möhnethal); (4) *A. Coitana*, K. ♀ ♂, s. and c.p. (Sauerland); (5) *Halictus villosulus*, K. ♀, c.p., ab.; (6) *H. leucozonius*, Schr. ♀, c.p.; (7) *H. cylindricus*, F. ♀, c.p., ab.; (8) *H. albipes* F. ♀ (obovatus, K.), c.p.; (9) *H. Smeathmanellus*, K. ♀, c.p.; (b) *Tenthredinidæ*: (10) *Tenthredo* sp., s. B. Diptera—(a) *Bombylidæ*: (11) *Systoechus sulfureus*, Mikan, s. (Sld.); (b) *Syrphidæ*: (12) *Cheilosia* sp.; (13) *Melithreptus tæniatus*, Meig., f.p. and s. (its stomach was quite full of a yellow mass of honey mixed with pollen); (14) *Volucella pellucens*, L., s., freq. (Sld.); (15) *Sericomyia lappona*, L., s. (Sld.); (16) *Eristalis horticola*, Deg., f.p. and s. (Sld.), ab.; (17) *E. arbustorum*, L., f.p. and s., very ab.; (c) *Conopidæ*: (18) *Sicus ferrugineus*, L., s. C. Lepidoptera—*Rhopalocera*: (19) *Hesperia silvanus*, Esp., s.

## 273. LEONTODON (THRINCIA) HIRTUS, L.:—

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus confusus*, Schenck, ♂, s.; (2) *Panurgus calcaratus*, Scop. ♀ ♂, c.p. and s., ab.; (3) *Rhophites vulgaris*,

Schenck, ♀, c.p. and s.; (4) *Cilissa melanura*, Nyl. ♀; (5) *Andrena denticulata*, K. ♀, s. and c.p. (Sld., Thur.); (6) *A. fulvicrus*, K. ♀, c.p.; (7) *A. fulvescens*, Sm. ♀, c.p. (Thur.); (8) *A. fulvago*, Chr. ♀, c.p. (Thur.); (9) *Halictus villosulus*, K. ♀, c.p.; (10) *H. leucozonius*, Schr. ♀ ♂, c.p. and s., very ab. (Thüringer Wald, August 30, 1869); (11) *H. cylindricus*, F. ♀ ♂, c.p. and s.; (12) *H. maculatus*, Sm. ♂, s.; (13) *H. Smeathmanellus*, K. ♀, c.p.; (14) *H. flavipes*, F. ♂, s.; (15) *H. lugubris*, K. ♂, s. B. Diptera—*Syrphidæ*: (16) *Eristalis arbustorum*, L., s. and f.p.; (17) *E. tenax*, L., do., both species ab.; (18) *Syrphus balteatus*, Deg., do. C. Lepidoptera—*Noctuæ*: (19) *Plusia gamma*, L., s. (as late as Oct. 14). See also No. 590, III.

274. *TARAXACUM OFFICINALE*, L.—The capitulum consists of about 100 to over 200 florets inserted on a receptacle only 5 to 7 mm. in diameter. In each floret the tube is 3 to 7 mm. long and the limb 7 to 15 mm. long, and in sunny weather the capitulum expands to form a bright yellow surface 30 to over 50 mm. in diameter. At night and in dull weather the capitulum closes up so completely that only the green involucre bracts and the dark outer surfaces of the limbs of the outermost florets remain visible. The honey rises into the upper part of the tube (which is nearly filled by the style), and is therefore accessible to insects with very short proboscides. From each tube an anther-cylinder  $2\frac{1}{2}$  to 5 mm. long protrudes, and the style grows to a height of 3 to 5 mm. above the anther-cylinder. The projecting portion of the style is clothed with pointed hairs over its whole outer surface, which retain entangled among them the pollen that they have swept out of the anther-cylinder. The two branches of the style, which are closely covered over their whole inner surfaces with stigmatic papillæ, are  $1\frac{1}{2}$  to over 2 mm. long; they bend outwards and curve so far back that the tip of each makes  $1\frac{1}{2}$  spiral turns, and accordingly, if insect-visits have not taken place and the sweeping-hairs are still covered with pollen, self-fertilisation must take place to a great extent.

Thus in the Dandelion we have a plant which, by the great conspicuousness of its flowers and the great abundance and accessibility of its pollen and honey, attracts an immense variety of insects in sunny spring weather; but which has fully retained, or has again acquired, the possibility of self-fertilisation, since it begins to bloom so early that as a rule its first flowers receive no insect-visits, while its latest flowers are also liable to be left unvisited.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, s. and c.p., very ab.; (2) *Bombus silvarum*, L. ♀; (3) *B. terrestris*, L. ♀; (4) *B. muscorum*, F. ♀; (5) *B. lapidarius*, L. ♀; (6) *B. confusus*, Schenck, ♀; (7) *B. Barbutellus*,

K. ♀; (8) *B. vestalis*, Fourc. ♀, all s.; (9) *Andrena cingulata*, K. ♂; (10) *A. cineraria*, L. ♀ ♂; (11) *A. pratensis*, Nyl. ♀; (12) *A. nitida*, K. ♀ ♂; (13) *A. albicans*, K. ♀ ♂, very ab.; (14) *A. fulva*, Schr. ♀; (15) *A. Gwynana*, K. ♀ ♂, very ab.; (16) *A. helvola*, L. ♀ ♂, not rare; (17) *A. mixta*, Schenck, ♀ (var. of the former); (18) *A. varians*, Rossi, ♀, not rare; (19) *A. atriceps*, K. ♀ ♂; (20) *A. nigroænea*, K. ♀; (21) *A. Trimmerana*, K. ♀; (22) *A. Smithella*, K. ♀ ♂, ab.; (23) *A. fulvicrus*, K. ♀ ♂, very ab.; (24) *A. fasciata*, Wesm. ♀ ♂; (25) *A. albicrus*, K. ♀ ♂; (26) *A. parvula*, K. ♀ ♂, very ab.; (27) *A. argentata*, Sm. (*gracilis*, Schenck), ♂, ab.; (28) *A. dorsata*, K. ♀ ♂, ab.; (29) *A. fulvescens*, Sm. ♀; (30) *A. connectens*, K. ♀; (31) *A. convexuscula*, K. ♀, all *Andrenæ* ♀ c.p. and s., the ♂ s.; (32) *Halictus rubicundus*, Chr. ♀; (33) *H. zonulus*, Sm. ♀; (34) *H. sexnotatus*, K. ♀, ab.; (35) *H. sexsignatus*, Schenck, ♀, ab. (as late as Oct. 13); (36) *H. maculatus*, Sm. ♀; (37) *H. albipes*, F. ♀, ab.; (38) *H. cylindricus*, F. ♀, ab.; (39) *H. flavipes*, F. ♀; (40) *H. morio*, F. ♀; (41) *H. leucopus*, K. ♀; (42) *H. longulus*, Sm. ♀; (43) *H. nitidiusculus*, K. ♀, ab.; (44) *H. villosulus*, K. ♀; (45) *H. lucidulus*, Schenck, ♀; (46) *H. nitidus*, Schenck, ♀; (47) *H. minutissimus*, K. ♀, all c.p. and s.; (48) *Sphécodes gibbus*, L. ♀, s.; (49) *Nomada ruficornis*, L. ♀ ♂, very ab.; (50) *N. varia*, Pz. ♀ ♂, ab.; (51) *N. Lathburiana*, K. ♀; (52) *N. flavoguttata*, K. ♂; (53) *N. lineola*, Pz. ♀; (54) *N. alternata*, K. ♀; (55) *N. succincta*, Pz. ♀ ♂; (56) *N. signata*, Jur. ♀ ♂, all s.; (57) *Osmia rufa*, L. ♂, s.; (58) *O. fusca*, Chr. (bicolor, Schr.) ♀, s. and c.p.; (b) *Formicidæ*: (59) *Formica congerens*, Nyl. ♀, ab., s.; (c) *Tenthredinidæ*: (60) *Cephus*, a small sp., ab. B. Diptera—(a) *Empidæ*: (61) *Empis livida*, L., ab.; (62) *E. punctata*, F., ab.; (63) *E. opaca*, F., all three s.; (b) *Syrphidæ*: (64) *Eristalis æneus*, Scop.; (65) *E. arbustorum*, L.; (66) *E. nemorum*, L.; (67) *E. tenax*, L. (as late as Oct. 13); (68) *E. pertinax*, Scop.; (69) *E. sepulcralis*, L.; (70) *E. intricarius*, L., all s. and f.p., ab.; (71) *Rhingia rostrata*, L.; (72) *Ascia lanceolata*, Mgn., s.; (73) *A. podagrica*, F., ab., f.p.; (74) *Syrphus nitidicollis*, Mgn., f.p.; (75) *S. pyrastris*, L., f.p.; (76) *Melithreptus tæniatus*, Mgn., f.p.; (77) *Cheilosia vernalis*, Fallen, f.p.; (78) *Ch. chloris*, Mgn., f.p.; (c) *Muscidæ*: (79) *Scatophaga stercoraria*, L.; (80) *Sc. merdaria*, F., both species s. and f.p., ab.; (81) *Onesia floralis*, R. D., freq. C. Lepidoptera—*Rhopalocera*: (82) *Vanessa urticæ*, L., ab.; (83) *V. Io*, L., ab.; (84) *Rhodocera rhamni*, L.; (85) *Pieris brassicæ*, L.; (86) *P. napi*, L.; (87) *Satyrus Megæra*, L.; (88) *Hesperia alveolus*, Hb., all s. D. Coleoptera—(a) *Nitidulidæ*: (89) *Meligethes*, ab.; (b) *Buprestidæ*: (90) *Anthaxia nitidula*, L.; (c) *Malacodermata*: (91) *Malachius bipustulatus*, F., f.p.; (d) *Coccinellidæ*: (92) *Coccinella septempunctata*, L., tries in vain to reach the honey. E. Hemiptera; (93) *Pyrocoris aptera*, L., s., ab. See also No. 590, III., for a further list of visitors in Low Germany; and No. 609 for a list of Alpine visitors.

Altogether I have observed upon the Dandelion—

	Apidæ	Lepidoptera.	Diptera.	Other Insects
In Low Germany ...	67	7	25	16
On the Alps ...	25	35	26	12

In each 100 visitors there are therefore—

	Apidæ	Lepidoptera.	Diptera.	Other Insects.
In Low Germany ...	58·2	6·1	21·7	13·9
On the Alps ...	25·5	35·7	26·5	12·2

### 275. *SONCHUS OLERACEUS*, L. :—

Visitors : A. Diptera—*Syrphidæ* : (1) *Syrphus balteatus*, Deg., f.p. ; (2) *S. arcuatus*, Fall. ; (3) *Eristalis arbustorum*, L. ; all three species s. and f.p. B. Lepidoptera—*Rhopalocera* : (4) *Pieris brassicæ*, L., s.

### 276. *SONCHUS ARVENSIS*, L. :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. and c.p., very ab., it dusts itself over and over with pollen ; (2) *Bombus* sp., s. ; (3) *Panurgus calcaratus*, Scop. ♀ ♂, s. and c.p., very ab. ; (4) *P. Banksianus*, K. ♀ ♂, scarcer ; (5) *Halictus quadricinctus*, F. ♀, c.p. ; (6) *H. rubicundus*, Chr. ♀, c.p. and s. ; (7) *H. flavipes*, F. ♀, c.p. ; (8) *H. lugubris*, K. ♂, s. ; (9) *Nomada varia*, Pz. ♀, s. ; (10) *Megachile centuncularis*, L. ♀, c.p. and s. ; (11) *Osmia spinulosa*, K. ♀, c.p. and s. (Thur.) B. Diptera—(a) *Syrphidæ* : (12) *Eristalis tenax*, L. ; (13) *E. arbustorum*, L., both species s. and f.p., ab. ; (14) *Cheilosia* sp., f.p. ; (b) *Conopidæ* : (15) *Sicus ferrugineus*, L., s. C. Lepidoptera—*Rhopalocera* : (16) *Hesperia* sp., s. D. Coleoptera—(a) *Curculionidæ* : (17) *Spermophagus cardui*, Schll., very numerous ; (b) *Malacodermata* : (18) *Malachius* sp., f.p.<sup>1</sup>

<sup>1</sup> The following additional Composites are discussed in my *Alpenblumen* (609) :—*Achillea atrata*, L., *A. macrophylla*, L., *A. moschata*, Wlf., *A. nana*, L., *Adenostyles albifrons*, Rehb., *A. alpina*, Bl. et Fing., *A. hybrida*, D.C., *Aronicum Clusii*, All., *Aster alpinus*, L., *Bellidiastrum Michelii*, Cass., *Carduus Personata*, Jacq., *Centaurea Mureti*, Jord., *C. nervosa*, Willd., *C. phrygia*, L., *Chrysanthemum alpinum*, L., *C. coronopifolium*, Vill., *Cnicus heterophyllus*, All., *C. spinosissimus*, Scop., *Crepis aurea*, Cass., *Gnaphalium dioicum*, L., *G. Leontopodium*, Scop., *Hieracium albidum*, L., *H. aurantiacum*, L., *H. Auricula*, L., *H. glanduliferum*, Vill., *H. staticifolium*, Vill., *H. villosum*, L., *Hypochaeris uniflora*, Vill., *Lactuca perennis*, L., *Lappa major*, Gärtn., *Mulgedium alpinum*, Cass., *Saussurea alpina*, D.C., *Senecio abrotanifolius*, L., *S. carniolicus*, Willd., *S. cordatus*, Koch., *S. Doronicum*, L., *S. nebrodensis*, L.

In addition to these, the following are treated in my *Weitere Beobachtungen*, pt. III. :—*Bidens cernua*, L., *Inula britannica*, L., *I. Helenium*, L., *I. hirta*, L., *Petasites officinalis*, Mönch., *Prenanthes muralis*, L., *P. purpurea*, L., *Senecio silvaticus*, L., *S. viscosus*, L., *Silybum Marianum*, L., *Sonchus asper*, Vill.

Besides all these, Hildebrand in his *Geschlechtsverhältnisse bei den Compositen* (357) treats of the following :—*Agathaea*, *Arctotis*, *Cacalia*, *Calendula*, *Cryptostemma*, *Dahlia*, *Doronicum*, *Gazania*, *Jurinea alata*, *Liatris*, *Melampodium divaricatum*, *Senecio populifolius*, *Silphium doronicifolium*, *Telekia*, *Vernonia*, *Xeranthemum*.

## REVIEW OF COMPOSITÆ.

A review of the Composites which I have more particularly described shows that the special characters of the family for the most part secure such abundant insect-visits that the power of self-fertilisation may be dispensed with; and to a great extent it has been dispensed with, though in this respect all gradations are found between such conspicuous and abundantly-visited forms as *Taraxacum*, *Cnicus arvensis*, and *Achillea*, and those which, like *Senecio vulgaris*, are only visited exceptionally, and regularly fertilise themselves.

Species in this last condition explain how it could be of advantage to one offshoot of the Senecionidæ with still less conspicuous flowers, viz. the Artemisiaceæ, to adapt themselves for wind-fertilisation, and to renounce entirely the insect-visits whose occurrence had become so rare. Delpino has shown in a masterly way in his work on the Artemisiaceæ, the small steps by which this change took place.

A comparison of species in the same genus (e.g. *Senecio Jacobæa* and *S. vulgaris*, *Carduus crispus* and *C. acanthoides*, *Cnicus arvensis*, *C. palustris*, and *C. nutans*), or of closely allied genera, shows clearly that in the Compositæ, as in other cases, the abundance of insect-visitors increases with the conspicuousness of the flowers, and the variety of insects with the accessibility of the honey. It is only in a few forms with solitary, inconspicuous capitula, devoid of ligulate marginal florets (*Gnaphalium uliginosum*, *Senecio vulgaris*), that insect-visits, and consequently cross-fertilisation, are rare.

If we compare in regard to the variety of insect-visitors, not isolated genera (*Salix*, *Scabiosa*, *Jasione*), but whole families, with the Compositæ, we find that the Umbelliferae alone rank with them; indeed they in some cases surpass in this respect the most favoured Composites. But corresponding to the different conditions of the honey in these two orders, there is this remarkable distinction, that the Umbelliferae are visited and fertilised mainly by those insects which are least specialised for floral nutriment, while most Compositæ are to a greater extent or even principally, visited by the most specialised orders of insects. To make this distinction quite evident, I have arranged in the following table ten of the commonest forms of each order with their visitors, choosing plants with whose insect-visitors I was best acquainted.

## INSECT-VISITORS OF COMMON COMPOSITÆ AND UMBELLIFERÆ.

	Total No. of species.	Percentages.							
		Lepidoptera.	Apida.	Diptera.	Other Insecta.	Lepidoptera.	Apida.	Diptera.	Other insects
COMPOSITÆ.									
<i>Taraxacum officinale</i> ... ..	93	7	58	21	7	7.5	62.5	22.6	7.4
<i>Cirsium arvense</i> ... ..	68	7	32	24	25	7.9	36.4	27.3	28.4
<i>Achillea Millefolium</i> ... ..	87	6	30	21	30	6.9	34.5	24.1	34.5
<i>Chrysanthemum leucanthemum</i> ...	72	5	12	28	27	6.9	16.6	38.9	37.5
<i>Centaurea Jacea</i> ... ..	48	13	28	6	1	27	58.7	12.5	2
<i>Carduus scanthoides</i> ... ..	44	4	32	3	5	9.1	72.7	6.8	11.3
<i>Senecio Jacobina</i> ... ..	40	3	16	18	3	7.5	40	45	7.5
<i>Pteris hieracioides</i> ... ..	29	3	16	9	1	10.3	55.2	31	3.4
<i>Tanacetum vulgare</i> ... ..	27	5	7	7	8	18.5	25.9	25.9	29.6
<i>Eupatorium cannabinum</i> ...	18	9	2	6	1	50	11.1	33.3	5.5
UMBELLIFERÆ.									
<i>Heracleum Sphondylium</i> ... ..	118	0	13	49	56	0	11.	41.5	47.4
<i>Ægopodium Podagraria</i> ... ..	104	0	15	34	55	0	14.4	32.6	52.9
<i>Anthriscus silvestris</i> ... ..	73	0	5	26	42	0	6.7	35.6	57.5
<i>Daucus Carota</i> ... ..	61	2	8	19	32	3.3	18.1	31.1	52.5
<i>Carum Carui</i> ... ..	55	1	9	21	24	1.8	16.4	38.2	43.6
<i>Anethum graveolens</i> ... ..	46	0	6	15	23	0	13	32.6	54.3
<i>Sium latifolium</i> ... ..	32	0	0	20	12	0	0	62.5	37.5
<i>Angelica silvestris</i> ... ..	30	1	2	11	16	3.3	6.6	36.6	53.3
<i>Cherophyllum temulum</i> ... ..	23	0	0	10	12	0	4.3	48.5	52.2
<i>Pimpinella Saxifraga</i> ... ..	23	0	3	8	12	0	13	34.8	52.2

This table shows clearly :—

1. That many Umbelliferæ are not visited at all by Lepidoptera, and the others to a small extent only; while the Compositæ are regularly visited by Lepidoptera, and in some cases (*Eupatorium*) depend mainly upon them. Of the ten Umbelliferæ, three only are shown to be visited by Lepidoptera, which in no case exceed 3·5 per cent. of the insect-visitors; and I can testify that even these few species are not regular but only exceptional guests. Of the ten Compositæ, all are visited by some Lepidoptera (7 to 50 per cent.), and these are among their regular visitors. *Eupatorium* I have found to be visited by very numerous Lepidoptera belonging to nine species.

2. Bees are among the visitors of almost all Umbelliferæ; but they only amount to a small number of species (under 16 per cent.), and to a still smaller percentage of individuals. They belong almost entirely to those genera which are either the least or the most adapted for obtaining honey (cf. p. 287). On the other hand, the flowers of Compositæ, richer in honey and in pollen, attract far more species of bees of the most various genera; so that in these ten Compositæ of my table, bees form 11 to 72 per

cent. of the whole number of species, and a still larger proportion of the individual visitors, and owing to their diligence they are of even greater importance in the work of fertilisation than this percentage directly indicates.

3. Diptera, and short-lipped insects of other orders (especially Hymenoptera and Coleoptera), form a considerable percentage of the species of visitors in both families, but more so in the case of Umbelliferæ than of Compositæ. In the ten Composites the number of Dipterous visitors varies from 6 to 45, in the ten Umbellifers from 31 to 62, per cent. Similarly, the percentage of short-lipped visitors of other orders varies in these Composites from 2 to 37, in the Umbellifers from 37 to 57, per cent. Diptera and short-lipped insects of other orders taken together make in the Compositæ 14 to 76, in the Umbelliferæ 83 to 100 per cent.

In the face of this evidence, it is unnecessary to discuss Delpino's statement (178, 180) that the Compositæ are fertilised almost exclusively by bees.

#### ORD. *STYLIDIEÆ*.

The plants of this order, according to Delpino (who examined only dried specimens), are markedly proterandrous and are evidently fertilised by insects (178).

#### ORD. *GOODENOVIEÆ*.

In the plants of this order the style ends in a collecting-cup, which receives the pollen while still in the bud and then closes up, leaving only a narrow opening for the most part covered by hairs. At the same time it bends down to stand in the mouth of the almost horizontal flower, so that insect-visitors come in contact with the hairs and dust themselves with a little of the powdery pollen. As the stigmatic lobes grow up in the cup they keep forcing fresh pollen into the narrow slit, and finally emerge by it themselves, and then receive the pollen of younger flowers from insect-visitors (178, 360, 550). The structure of the stigma in the different genera (*Goodenia*, *Scevola*, *Velleia*, *Calogyne*, *Dampiera*, *Leschenaultia*) is very variable, as Bentham shows in an interesting paper (84). In *Leschenaultia formosa*, R. Br., the insect's proboscis comes in contact with the lower lip of the pollen-cup, thus opening it and dusting itself with pollen; in the next flower it places this pollen on the stigmatic surface which lies outside the pollen-cup (Darwin, No. 162).

ORD. *CAMPANULACEÆ*.Tribe *Lobeliæ*.

*Siphocampylus bicolor*, G. Don.—The five anthers cohere to form a hollow cylinder which becomes filled with pollen, and whose anterior opening bends downwards into the mouth of the flower. In the first stage the style, with its two stigmatic lobes closely applied to one another, extends to the base of the anther-cylinder, but gradually grows up through it, brushing the pollen before it out of the cylinder by means of a ring of hairs placed behind the stigmas. When the stigmas issue at the anterior opening of the cylinder the two lobes separate and expose their papillar surfaces to contact with insect-visitors in the upper part of the mouth of the flower. So insects come in contact in younger flowers with pollen at the anterior opening of the anther-cylinder, and in older flowers with the stigmas, and regularly fertilise older flowers with the pollen of younger (Hildebrand, Nos. 346 and 351).

Other species of *Siphocampylus* are believed by Delpino to be fertilised by honey-sucking birds (178).

*Isotoma axillaris*, R. Br.—The mechanism is for the most part similar, but there is a lancet-like appendage to each of the lower anthers which extends downwards into the upper part of the flower, and which causes shedding of the pollen when touched by an insect (Hildebrand, No. 356).

*Lobelia Erinus*, L. (?) (Common Blue Lobelia).—The flower, which has been thoroughly described by Mr. T. H. Farrer, agrees in all essential points with *Siphocampylus bicolor*, and is visited by bees (240).

Delpino saw *Lobelia Erinus* visited by *Halictus* (178). Hildebrand observed in the same species that the style is frequently not able to force its way through the closed end of the anther-tube, and that in such a case the stigmatic lobes unfold within the anther-tube and are self-fertilised (360).

*Lobelia syphilitica*, L., is abundantly visited by *Bombus italicus* and *B. terrestris* (Delpino, 172, 176).

*Lobelia fulgens*, Willd.—Delpino suggested that this plant is fertilised by humming-birds (172, 176), and Trelease afterwards saw the flowers visited by the Ruby-throated Humming-bird (727, 751).

*Heterotoma* differs from *Siphocampylus* in having all the lobes of the corolla bent downwards, in the lower portion of the corolla being

produced into a long spur, and in the stamens only cohering for a short distance below the anthers (360).

Tribe *Cyphicæ*.

The stigma is crowned with a tuft of hairs and only reaches to the base of the anthers, which are closely aggregated together and contain the pollen in a single large mass between them. The anthers stand on the lower side of the horizontal flowers, and separate when the insect-visitor enters, so that the ventral surface of the insect comes in contact with the pollen and with the stigma. Bees are probably the fertilising agents (178, 360).

Tribe *Campanuleæ*.

The structure of the flower in our species of *Campanula* has been admirably described and explained by Sprengel. Delpino makes general remarks upon this and several other genera of *Campanuleæ*, and names *Cetoniæ* as the fertilisers of *Campanula Medium*, and *Apis* and *Halictus* as fertilisers of the other species of *Campanula*; and he gives in addition to his own observations a full account of the erroneous views of Wahlbom, Cassini, Du Petit-Thouars, Alph. de Candolle, Treviranus, Gärtner, and Vaucher concerning the fertilisation of *Campanula* (178, 360).

In *Campanula* the honey is secreted and borne by a yellow, fleshy, epigynous disk (*n*), surrounding the base of the style; it is covered by the bases of the five stamens which expand in triangular laminæ (*sd*). Hairs close over the interspaces between the bases of the stamens, and protect the honey rather from unbidden guests than, as Sprengel supposes, from rain, which is sufficiently guarded against in most species by the pendulous position of the flowers.

In the bud, and often for a time in the open flower, the three stigmas lie closely applied together, forming a cylinder whose outer surface is thickly covered with long, erect hairs; in the bud the anthers are placed close around this cylindrical brush (*grb*), so that they form a hollow cylinder inclosing the style, and as they dehisce introrsely they shed their pollen upon the hairs of the brush. When this has taken place the stamens wither and withdraw into the base of the flower. Now the flower opens and displays in the first stage of its development a cylindrical brush standing in the centre and covered thickly all round with pollen,

which is rubbed off by the hairy bodies of insect-visitors until it is exhausted; meanwhile the hairs of the brush gradually shrivel. In the second stage the three divisions of the style separate and curve backwards, exposing their inner surfaces covered with stigmatic papillæ (*st*) to be touched by insect-visitors. In case of sufficient insect-visits, cross-fertilisation, and, as in every case of marked proterandry, fertilisation of older flowers with the pollen of younger, is inevitable.

In *Campanula*, when insects have not visited the flower to a sufficient extent, the stigmas usually bend further backwards

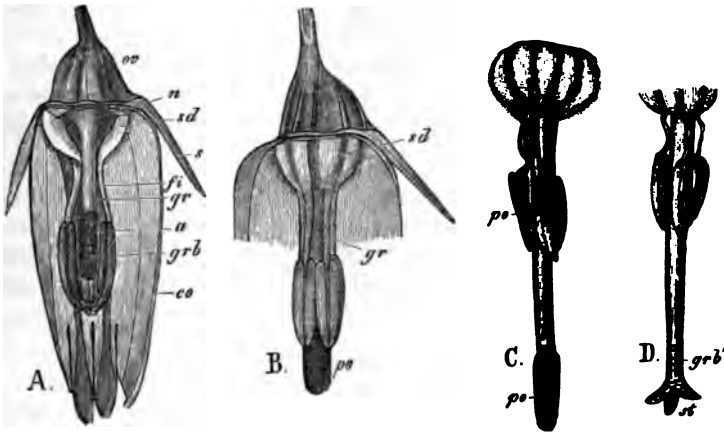


FIG. 113.—*Campanula pusilla*, L.

- A.—Section of young bud.  
 B.—Essential organs of a bud about to open.  
 C.—Essential organs of a flower, in first (male) stage.  
 D.—Ditto, in second (female) stage. ( $\times 4$ .)  
*sd*, expanded bases of the filaments, fringed with hairs, which guard the honey; *grb*, brush upon the style; *grb'*, ditto, after its hairs have shrivelled up.

until self-fertilisation is effected. The papillose end of the stigma either comes in immediate contact with the pollen still adhering to the upper end of the styles, or pollen falls of itself upon the papillæ of the recurved portion. It is clear from its wide, bell-shaped corolla, that *Campanula* is specially adapted for humble-bees, but the flowers in the various species are visited by many other insects, chiefly bees. Many insects find shelter from rain and also spend the night within the flowers; and some confine their visits mainly (*Cilissa hæmorrhoidalis*, species of *Chelostoma*) or almost exclusively (*Halictoides dentiventris*) to species of *Campanula*.

277. *CAMPANULA ROTUNDIFOLIA*, L. :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. ; (2) *Bombus pratorum*, L. ♀, s. ; (3) *B. lapidarius*, L. ♀, c.p. ; (4) *Cilissa hæmarrhoidalis*, F. ♀ ♂, s. and c.p. ; (5) *Andrena Coitana*, K. ♂ (Sld.), ab. ; (6) *A. Gwynana*, K. ♂ ; (7) *Halictus Smeathmanellus*, K. ♂ ; (8) *Halictoides dentiventris*, Nyl. ♂ ♀, the ♂ abundant, sometimes passing the night within the flowers ; (9) *Chelostoma nigricorne*, Nyl. ♀ ♂, s. and c.p. ; (10) *Ch. Campanularum*, L., do. B. Diptera—(a) *Bombylidæ* : (11) *Systæchus sulfureus*, Mik., s. (Sld.) ; (b) *Empidæ* : (12) *Rhamphomyia plumipes*, Fallen, ab. C. Lepidoptera—(13) *Ino statices*, L., s. (Sld.). D. Coleoptera—(a) *Staphylinidæ* : (14) *Anthobium* ; (b) *Curculionidæ* : (15) *Gymnetron Campanulæ*, L. ; (16) *Otiorhynchus ovatus*. On the Alps also this species is chiefly visited by bees (609). See also No. 590, III.

278. *CAMPANULA TRACHELIUM*, L. :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L., ♀, s., ab. ; (2) *Cilissa hæmarrhoidalis*, F. ♀ ♂, s. and c.p., the ♂ very ab., sometimes three in one flower ; (3) *Andrena Coitana*, K. ♀ ♂, here also the ♂ is much the more abundant ; (4) *A. Gwynana*, K. ♀ ♂, ab. ; (5) *A. fulvicrus*, K. ♂, taking shelter during rain ; (6) *Halictus cylindricus*, F. ♀, c.p. ; (7) *Halictoides dentiventris*, Nyl. ♀ ♂, ♂ very ab. ; (8) *Prosopis hyalinata*, Sm. ♀ ♂, ab. ; (9) *Chelostoma Campanularum*, L. B. Diptera—*Syrphidæ* : (10) *Chrysoschlamys ruficornis*, F. (Lippstadt, Sld.), f.p. ; (11) *Syrphus balteatus*, Deg., f.p. C. Coleoptera—(a) *Nitidulidæ* : (12) *Meligethes*, very ab. ; (b) *Cryptophagidæ* : (13) *Antherophagus*, sp. See also No. 590, III.

279. *CAMPANULA RAPUNCULOIDES*, L. :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. ; (2) *Bombus lapidarius*, L. ♀, s. and c.p. ; (3) *Cilissa hæmarrhoidalis*, F. ♀ ♂ ; (4) *Andrena Gwynana*, K. ♂ ♀ ; (5) *Halictus maculatus*, Sm. ♂ ; (6) *H. albipes*, K. ♀ ; (7) *Chelostoma nigricorne*, Nyl. ♂ ♀ ; (8) *Ch. Campanularum*, K. ♂ ♀ ; (9) *Prosopis hyalinata*, Sm. ♂ ♀, the last three ab. B. Diptera—*Syrphidæ* : (10) *Rhingia rostrata*, L., s., it issues from the flower with its back covered with pollen. See also No. 590, III.

280. *CAMPANULA BONONIENSIS*, L. (Wandersleber Gleiche in Thuringia).

Visitors : A. Hymenoptera—*Apidæ* : (1) *Chelostoma florissomne*, L. ♀ ♂, freq. ; (2) *Ch. nigricorne*, Nyl. ♀ ♂ ; (3) *Ch. Campanularum*, K. ♀ ♂, ab. ; (4) *Halictus flavipes*, F. ♀. B. Coleoptera—*Nitidulidæ* : (5) *Meligethes*, freq. See also No. 590, III.

281. *CAMPANULA PATULA*, L. :—

Visitors : Hymenoptera—*Apidæ* : (1) *Andrena Gwynana*, K. ♀, s. and c.p. ; (2) *Chelostoma nigricorne*, Nyl. ♂ ♀, s. and c.p. See also No. 590, III.

282. *CAMPANULA PERSICIFOLIA*, L. :—

Visitors: A. Hymenoptera—*Apidæ*: (1) *Prosopis hyalinata*, Sm. ♀ ♂. B. Orthoptera—(2) *Forficula auricularia*, L., hiding in the flowers. See also No. 590, III.

*Campanula canescens*, Wall., and *C. colorata*, Wall., two East Indian species, have cleistogamic flowers (531).<sup>1</sup>

*Specularia perfoliata*, Dec.—The cleistogamic flowers, which were known to Linnæus, are described by H. von Mohl (531).

*Trachelium*.—When the flower expands the pollen adheres to the hairs of the stigma, which in the bud grows up between the anthers; these hairs then wither and readily give up the pollen to an insect-visitor. Afterwards the stigma unfolds and its papillæ develop. Delpino observed a cabbage-white butterfly (*Pieris*) sucking, and a bee (*Halictus*) collecting pollen, on the flowers (178, 360).

*Phyteuma*.—The structure of the flower of *Phyteuma* resembles on the whole that of *Campanula*, but the pollen, as in *Compositæ*, is pushed up out of a tube by the growing style, and comes to lie outside the flower exactly in the spot where the stigmas afterwards unfold. The tube is formed by the long strap-shaped lobes of the corolla which cohere for a time and afterwards separate. This arrangement allows of diminution in size and aggregation of the flowers without interfering with the certainty of cross-fertilisation.

I have found the blue Alpine species of *Phyteuma* (*P. hemisphæricum*, L., *humile*, Schleich., *orbiculare*, L., *Scheuchzeri*, All., *Michelii*, All., *Halleri*, All.) to be visited for the most part by numerous bees and butterflies. For instance, on *P. Michelii* I observed seventeen *Apidæ* (including twelve humble-bees), forty-two *Lepidoptera*, eight *Diptera*, one beetle (No. 609, pp. 406-413).

*Phyteuma pauciflorum*, L., was found by Ricca to be visited by humble-bees on the Alps at a height of nearly 10,000 feet (665).

283. *JASIONE MONTANA*, L.—The structure of the flower was described thoroughly and accurately by Sprengel. The flower, to a greater extent even than *Phyteuma*, has two advantages over *Campanula*, for (1) it attracts much more numerous and more varied insects for the sake of its honey and pollen, and (2) it allows the larger visitors to fertilise a greater number of stigmas simultaneously with pollen from other flowers, while in *Campanula* the fertilisation of each flower requires a separate visit.

<sup>1</sup> The following additional species of *Campanula* are discussed in my *Alpenblumen*: *C. pusilla*, Hænk., *C. Scheuchzeri*, Vill., *C. barbata*, L., and *C. thyrsoides*, L.

The visits of a more miscellaneous lot of insects are attained by the honey being very easily accessible, though protected from rain. It is secreted, as in *Campanula*, by the upper surface of the ovary, where it lies fully exposed and surrounded by the flat limb of the calyx. The corolla is cleft to its base into narrow linear lobes, and permits the most short-lipped insects to have free access to the honey; the stamens, by cohering at the base of the anthers

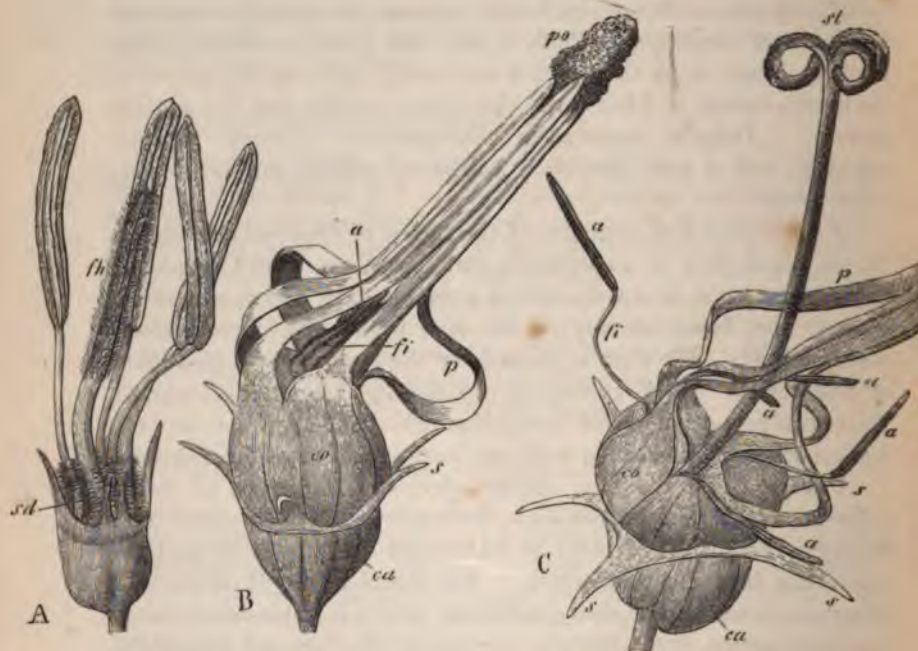


FIG. 119.—*Phyteuma Michelii*, L.

A.—Young bud, after removal of the corolla and of one stamen.

B.—Flower, in first (male) stage.

C.—Ditto, in second (female) stage. ( $\times 7$ )

(Franzensshöh, July 20, 1874).

to form a ring round the style, shelter the honey from rain, though not from insects, which can insert their heads or tongues between the filaments which are quite thin and widely separate to their bases. Drops of rain are excluded from the base of the flower partly by the shrivelled anthers which point obliquely upwards, and partly by the filaments. That the larger insects fertilise numerous flowers at each visit with pollen from other flowers is effected by three other characters conjointly. In the first place, the flowers

are so small and so closely aggregated that the larger insects come in contact with many at once in their visits; secondly, the styles elongate until they overtop the lobes of the corolla; and thirdly, here as in *Campanula* the flowers are markedly protogynous, the style bearing first a cylindrical brush covered with pollen (Fig. 120, 3), and afterwards, when both pollen and hairs have

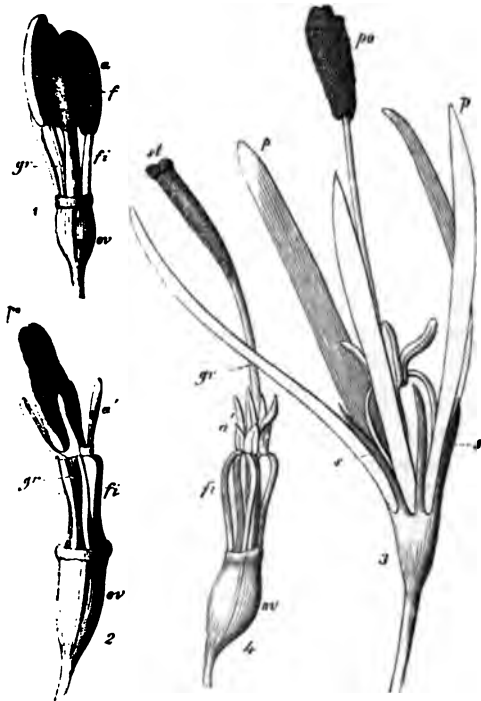


FIG. 120.—*Jasione montana*, L.

- 1.—Essential organs, from a young bud. The still closed anthers have been separated slightly, to show the style with its brush lying between them.
- 2.—Essential organs, of an older bud. The anthers have shed their pollen upon the style, and have shrivelled up into narrow lobes which remain coherent at their base.
- 3.—Flower, in first (male) stage.
- 4.—Ditto, in second (female) stage, after removal of the calyx and corolla.

disappeared, displaying a two-lobed stigma. The small size of the flowers is fully compensated for by the union of a large number in a capitulum. Sprengel states the number of florets in a capitulum to be about seventy; in the specimens that I have examined, I have found the number to be considerably over 100, even reaching 180.

*Jasione* is rendered especially conspicuous by growing chiefly on dry, sandy soil, where it is usually one of the most prominent flowers, and where many bees and sand-wasps which visit it have their nests.

On two such spots, behind the Tannenbaum at Lippstadt, and on the Lippstadt Heath, I found the following insects visiting the flowers in July and August, 1868 and 1869 :—

- A. Hymenoptera—(a) *Apidae* : (1) *Bombus hortorum*, L. ♀ ♂, s. ; (2) *B. silvarum*, L. ♀, s. ; (3) *B. rupestris*, L. ♀, s. ; (4) *Sarapoda bimaculata*, Pz. ♀ ♂, very ab., s. and c.p. ; (5) *Dasypoda hirtipes*, F. ♂, freq. ; (6) *Cilissa leporina*, Pz. ♀ ; (7) *Rhophites halictula*, Nyl. ♀, s. ; (8) *Andrena Hattorfiana*, F. ♂, once ; (9) *A. dorsata*, K. ♀ ♂, ab. ; (10) *A. pubescens*, K. ♂ (= *fuscipes*, K.), s. ; (11) *A. fulvago*, Chr. ♀ ; (12) *A. helvola*, L. ♀ ; (13) *A. fulvicrus*, K. ♀ ; (14) *A. argentata*, Sm. ♂ ; (15) *A. pilipes*, F. ♂ ; (16) *A. Coitana*, K. ♂ ♀ ; (17) *Colletes marginata*, L. ♂ ; (18) *Halictus fasciatus*, Nyl. ♀ ; (19) *H. flavipes*, F. ♂ ; (20) *H. leucozonius*, Schr. ♀ ; (21) *H. albipes*, F. ♀ ; (22) *H. cylindricus*, F. ♀ ♂ ; (23) *H. villosulus*, K. ♀ ; (24) *H. lucidulus*, Schenck, ♀ ; (25) *Sphecodes gibbus*, L. ♀ (var. *rufescens*, Fourc.) ; in the last three genera the ♂ s., the ♀ s. and c.p. ; (26) *Ceratina cærulea*, Vill. ♀ ♂, freq., s. and c.p. ; (27) *Nomada ruficornis*, L. ♀ ♂ ; (28) *N. Roberjeotiana*, Pz. ♀ ♂ ; (29) *N. nigrita*, Schenck, ♂ ; (30) *N. lineola*, Pz. ♂ ; (31) *N. Jacobææ*, Pz. ; (32) *N. varia*, Pz. ; (33) *N. Fabriciana*, L. ; (34) *Cœlioxys quadridentata*, L. ♀ ♂, ab. ; (35) *C. conoidea*, Ill. (punctata, Lep. ♀) ; (36) *C. simplex*, Nyl. ♀ ♂, s. ; (37) *Epeolus variegatus*, L. ♂ ♀, freq. ; the cuckoo-bees of course only suck ; (38) *Anthidium strigatum*, Latr. ♂ ; (39) *Diphysis serratulæ*, Pz. ♀ ; (40) *Megachile maritima*, K. ♂ ; (41) *M. argentata*, F. ♂ ♀, s. and c.p., ab. ; (42) *Chelostoma campanularum*, L. ♀ ; (43) *Prosopis variegata*, F. ♀ ♂, very ab. ; (44) *P. dilatata*, K. ♂ ; (45) *P. communis*, Nyl. ♀ ♂, ab. ; (46) *P. hyalinata*, Sm. ♀, ab. ; (47) *P. pictipes*, Nyl. ♀, scarce ; (b) *Sphegidae*, s. ; (48) *Ammophila sabulosa*, L. ♂, freq. ; (49) *Psammophila affinis*, K. ♂ ♀, very freq. ; (50) *Pompilus rufipes*, L. ♂ ; (51) *P. viaticus*, L. ♂ ; (52) *Ceropales maculata*, F., freq. ; (53) *Cerceris arenaria*, L. ♀ ♂, ab. ; (54) *C. labiata*, F. ♂ ; (55) *C. nasuta*, Kl. ♂ ; (56) *Mellinus sabulosus*, F., freq. ; (57) *Miscus campestris*, Latr. ♀ ; (58) *Philanthus triangulum*, F. ; (59) *Tachytes pectinipes*, L. ; (60) *Lindenius albilabris*, F. ; (61) *Oxybelus uniglumis*, L., ab. ; (62) *O. bellicosus*, Ol. ; (63) *O. mandibularis*, Dhlb. ; (64) *Crabro alatus*, Pz. ♀ ♂, very ab. ; (65) *Cr. patellatus*, v. d. L. ♀ ; (66) *Cr. pterotus*, F. ♀ ♂, both not rare ; (c) *Chrysidæ* : (67) *Hedychrum lucidulum*, Latr., s. B. Diptera—(a) *Bombylidæ* : (68) *Exoprosopa capucina*, F., not rare ; (b) *Empidæ* : (69) *Empis livida*, L., very ab. ; (c) *Syrphidæ* : (70) *Melithreptus scriptus*, L. ; (71) *M. menthastri*, L. ; (72) *Volucella bombylans*, L. ; (73) *Helophilus pendulus*, L. ; (74) *Eristalis tenax*, L. ; (75) *E. æneus*, Scop. ; (76) *E. arbustorum*, L. ; (77) *Syritta pipiens*, L. ; (78) *Melanostoma mellina*, L. ; (79) *Syrphus pyrastris*, L. ; (80) *Eumerus sabulonum*, Fall. ; (81) *Pipizella*, sp. ; (d) *Conopidæ* : (82) *Sicus ferrugineus*, L. ; (83) *Physocephala rufipes*, F., freq. ; (84) *Ph. vittata*, F. ; (e) *Muscidæ* : (85) *Ocyptera brassicaria*, F. ; (86) *O. cylindrica*, F., both very freq. ; (87) *Echinomyia tessellata*, F., very ab. ; (88) *E. ferox*, Pz. ; (89) *Oliviera lateralis*, Pz., ab. The *Syrphidæ* both s. and c.p., the others only s. C. Lepidoptera, s. ; (a)

*Rhopalocera* : (90) *Polyommatus Phlœas*, L., s., ab. ; (91) *P. Dorilis*, Hfn., freq. ; (92) *Lycæna ægon*, W. V. ♂ ; (93) *Satyrus Janira*, L., ab. ; (94) *S. pamphilus*, L. ; (95) *Hesperia thauumas*, Hfn. ; (b) *Sphingidæ* : (96) *Ino statices*, L. D. Coleoptera—(a) *Ædemeridæ* : (97) *Ædemera virescens*, L. ; (b) *Cerambycidæ* : (98) *Leptura livida*, L., freq., l.h. ; (c) *Chrysomelidæ* : (99) *Cryptocephalus sericeus*, L. A list of nineteen additional visitors is given in No. 590, III.

*Jasione montana* stands in the front rank of our native plants in regard to the number and variety of its insect-visitors ; it is only matched by some Umbelliferæ and Compositæ, which share with it the advantages of fully-exposed honey, and the union of numerous flowers with freely-projecting reproductive stigmas and anthers in a conspicuous inflorescence. In all such plants, cross-fertilisation is completely insured, and accordingly the possibility of self-fertilisation has been lost.

#### ORD. VACCINIACEÆ.

284. *VACCINIUM MYRTILLUS*, L. ; 285, *V. ULIGINOSUM*, L.—Both species are slightly proterandrous, and resemble *Erica tetralix* in their mode of fertilisation.

In *V. Myrtillus*, according to Sprengel, honey is secreted and borne by the white annular ridge or disk which rests upon the ovary and surrounds the style ; I have never found this disk moist, even when the wide part of the corolla is quite wet with honey ; it is moreover not so smooth as honey-glands usually are. On the other hand, I have very frequently found in both species a drop of honey at the outer side of the base of each stamen ; and as the base of the corolla immediately above its insertion is all round much thicker and fleshier than the upper portion, I at first did not doubt that it secreted the honey. But I have since convinced myself that Sprengel was right, and that the drops of honey secreted by the epigynous disk pass between the filaments to the wall of the corolla.

So far, both species agree with one another : but in other respects each has certain advantages over the other. *V. Myrtillus* secretes more honey, which is lodged in a much more globular corolla ; the opening is narrowed so that only insects with a proboscis long enough to reach from the exterior to the base of the corolla can obtain the honey. On the other hand, *V. uliginosum* forms taller bushes bearing much more numerous flowers, which are red on the side turned towards the light and therefore much more conspicuous while the mouth of the corolla is 3 mm. wide, permitting

the smaller insects to insert their heads or the whole forepart of the body. *V. Myrtillus* has thus adapted itself exclusively for the long-probosced bees (hive-bees, humble-bees), which are conspicuous for their skill and diligence; they know that within the inconspicuous corolla they will find a rich store of honey, and seek it so assiduously that hundreds of the flowers are visited and fertilised by a single insect. *V. uliginosum* has adapted itself by its more conspicuous flowers and more accessible honey to much more various insects; it is much less frequently and less assiduously visited by the long-tongued bees than *V. Myrtillus*, for the greater part of the honey is carried away by the short-lipped insects.

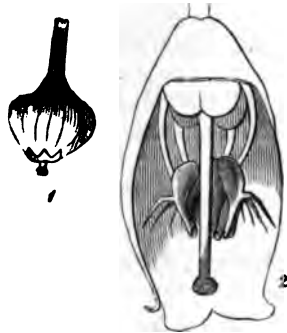


FIG. 121.

- 1.—Flower of *Vaccinium Myrtillus*, slightly magnified, from the side.
- 2.—Flower of *V. uliginosum*, after removal of half the corolla ( $\times 7$ ).

The difference in size of the mouths of the corolla causes also another difference, illustrated in Fig. 121. In *V. Myrtillus* the stigma projects a little beyond the corolla, and, as every insect-visitor inserts only its proboscis into the flower, the stigma is certain to be touched by the insect's head before the latter receives the pollen shed upon it. In *V. uliginosum*, if the stigma occupied the same position, the smaller bees (*Halictus* and small *Andrenæ* and *Nomadæ*) might enter the flower without ever touching the stigma; whereas, placed as it is, immediately within the entrance, it must be touched by even the smallest insects entering the flower. I have verified by direct observation this marked distinction between the insect-visitors of the two species.

## 284. V. MYRTILLUS, L.:—

Visitors: (1) *Apis mellifica*, L. ♀, very ab., s.; (2) *Bombus agrorum*, F. ♀, ab.; (3) *B. lapidarius*, L. ♀; (4) *B. terrestris*, L. ♀; (5) *B. Scrimshiranus*, K. ♀, all sucking only. They hung, head downwards, from the corolla. All the humble-bees that I observed were females, for the workers scarcely occur when the plant is in flower (middle of April to beginning of May). (6) *Andrena nigroænea*, K. ♂, I once found this species, whose proboscis is only  $3\frac{1}{2}$  mm. long, endeavouring vainly to reach the honey.

285. V. ULIGINOSUM, L.—I found all the following insects upon this plant on one sunny afternoon (May 19, 1870):—

A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, ab.; (2) *Bombus terrestris*, L. ♀, freq.; (3) *B. hortorum*, L. ♀; (4) *B. pratorum*, L. ♀; (5) *B. agrorum*, F. ♀; (6) *B. confusus*, Schenck, ♀; (7) *B. (Apathus) vestalis*, Fourc. ♀, freq.; (8) *B. (A.) campestris*, Pz. ♀; (9) *B. silvarum*, L. ♀; (10) *Andrena nigroænea*, K. ♂♂; (11) *A. pilipes*, F. ♂; (12) *A. fulva*, Schrank, ♀; (13) *A. Gwynana*, K. ♀; (14) *A. atriceps*, K. ♂; (15) *Halictus rubicundus*, Chr. ♀; (16) *H. flavipes*, F. ♀; (17) *H. sexnotatus*, K. ♀; (18) *H. cylindricus*, F. ♀; (19) *H. sexstrigatus*, Schenck, ♀; (20) *Colletes cunicularia*, L. ♀; (21) *Nomada ruficornis*, L. ♀; (22) *N. ferruginata*, K. ♀; (23) *Osmia rufa*, L. ♀, all sucking; (b) *Vespidae*: (24) *Vespa rufa*, L., s. B. Diptera—*Syrphidae*: (25) *Eristalis arbustorum*, L., very ab.; (26) *E. horticola*, Mgn., scarce; (27) *E. intricarius*, L., do.; (28) *Rhingia rostrata*, L., not unfreq.; all four sucking. C. Lepidoptera—*Rhopalocera*: (29) *Lycæna argiolus*, L.; (30) *Thecla rubi*, L., both sucking. See also No. 590, III.

*Vaccinium oxycoccus*, L.—The structure of the flower was carefully described by Sprengel. It is adapted for bees, but is very sparingly visited. The flowers last a very long time, according to Sprengel, eighteen days, and Sprengel was probably justified in considering this fact to be explained by the scanty insect-visits (590, III.).

*Vaccinium Vitis-idæa*, L.—The mouth of the corolla is still wider than in *V. uliginosum*, and the flower is more nearly erect. The plant is fertilised by hive-bees and humble-bees (589, 609).

## ORD. ERICACEÆ.

Tribe *Arbutæ*.

*Arctostaphylos Uva-ursi*, Spr. (*Arbutus uva-ursi*, L.).—The flower resembles that of *Erica tetralix* in structure, and is likewise fertilised chiefly by humble-bees (609).

Tribe *Andromedææ*.

*Epigæa* is *tetramorphic*, possessing four kinds of flowers, which differ partly in the length of the style, partly in the condition of the stigma and anthers (Asa Gray, No. 285).

Tribe *Ericææ*.

286. *ERICA TETRALIX*, L.—The pendulous, urceolate flower is 7 mm. long, 4 mm. wide in the middle, and 2 mm. wide at the



FIG. 122.—*Erica tetralix*, L.

Flower, after removal of half the calyx and corolla.

a, sepal; b, corolla; c, its recurved limb; d, anthers, partly displaced; e, their orifices; f, their appendages; g, nectaries; h, ovary; i, style; k, stigma.

mouth. The base of the ovary is surrounded by a dark, glandular ring which secretes honey. The style (i) stands in the axis of the flower, extending to the mouth of the corolla; it bears at the end a blackish, moist, sticky stigma (k), which protrudes slightly from the mouth of the flower, so that an insect, hanging beneath the flower and thrusting its proboscis towards the honey at the base, must bring the forepart of its head in contact with the stigma and be smeared with the sticky secretion. The eight anthers lie in a circle close around the style, a little way above the stigma (in the inverted position of the flower); each possesses two long, sharp, divergent processes, which reach to the sides of the

corolla. A honey-seeking insect, immediately after touching the stigma, brings its proboscis in contact with some of these appendages, whereupon a shower of dry, dusty pollen is shed from the holes in the anthers on to the forepart of the insect's head.

In absence of insects, self-fertilisation may take place, as part of the pollen always falls upon the edge of the stigma and remains adherent there. Humble-bees are the chief fertilising agents.

This species was described by Dr. Ogle in No. 633.

A. Hymenoptera—*Apidae*: (1) *Bombus senilis*, Sm. ♀ ♂ ♂ (14—15); (2) *B. silvarum*, L. ♀ ♂ (10—14); (3) *B. agrorum*, F. ♀ ♂ (10—15); (4) *B. Rajellus*, Ill. ♀ (10—11); (5) *B. terrestris*, L. ♀ (7—9), all very ab., hanging to the corolla back downwards; (6) *Nomada Solidaginis*, Pz. ♂, I saw this insect once, apparently trying in vain to reach the honey; (7) *Apis mellifica*, L. ♀, is scarcely able to reach the base of the flower legitimately, as its proboscis is only 6 mm. long. It is a very abundant visitor of *Erica tetralix*, but usually bites through the corolla, about midway. On Oct. 15, 1871, I saw numerous honey-bees sucking normally. I omitted to observe whether these late flowers were a little smaller than those of summer; if so they would exactly suit the honey-bee. B. Diptera—*Syrphidae*: (8) *Volucella bombylans*, L. (7—8), ab., s.; (9) *V. plumata*, L. freq., s.; (10) *V. hæmarrhoidalis*, Zett., scarce, s. C. Lepidoptera—*Noctua*: (11) *Plusia gamma*, L., s.

*Erica cinerea*, L., the fine-leaved heath, agrees in the structure of its flower with *E. tetralix*, according to Dr. Ogle (633).

*Erica carnea*, L.—This species is adapted by the colour and size of its flowers to butterflies, which alone (*e.g.* *V. cardui*) visit it in abundance, and effect cross-fertilisation. The sepals and petals vary from bright pink to crimson, and the peduncles are still more intensely coloured. The flower narrows so much towards its mouth that the entrance is blocked by the anthers, and just admits the thin proboscis of a butterfly, which cannot avoid touching first the stigma and then the anthers, and so performing cross-fertilisation. I have seen *Bombus terrestris* making great but ineffectual efforts to insert its proboscis into the flower. The inverted position of the flower is somewhat inconvenient for butterflies, and causes them delay. We may suppose that the ancestors of *Erica carnea* grew where bees were more plentiful and butterflies less so, and that the flowers were first adapted for bees, as almost all other inverted, bell-shaped flowers are; and that they acquired their present colour and form under the influence of Lepidoptera, which preponderate so conspicuously in the Alps (609).

287. *CALLUNA VULGARIS*, L.—The bell-shaped corolla is 2 to

3 mm. long, and cleft into four lobes to near its base. Honey is secreted by eight blackish glands in the base of the flower, alternating with the stamens, and is easily accessible to short-lipped insects. What the plant loses in attractiveness by the small

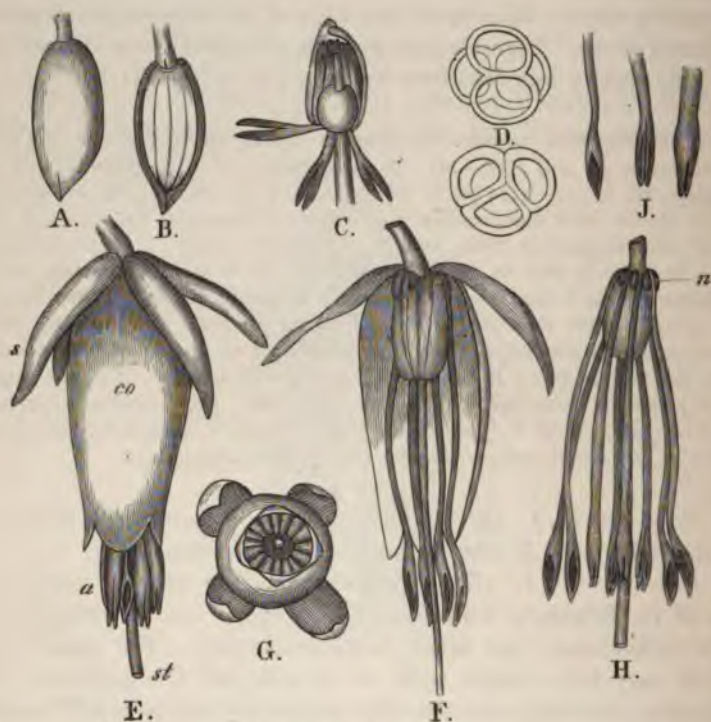


FIG. 123.—*Erica carnea*, L.

- A.—Bud for next year, inclosed in the calyx ( $\times 7$ ).  
 B.—Ditto, after removal of two sepals.  
 C.—Ditto, after removal of the whole calyx and half the corolla. Three of the eight stamens have been drawn out ( $\times 7$ ).  
 D.—Pollen-tetrads from a bud, greatly magnified. (Bergün, September 5, 1878.)  
 E.—Flower, in side view ( $\times 7$ ). The flowers usually do not hang vertically, but only inclined downwards.  
 F.—Ditto, after removal of half of the stamens and corolla.  
 G.—Mouth of flower.  
 H.—Essential organs, in their natural position; the stamens have sprung slightly outwards on removal of the corolla.  
 J.—Anthers; inner, outer, and lateral view.  
 (E, F, G, Lenz, June 1; H, J, Bergün, June 2, 1879).

size of its corolla, it makes up by the red colour and large size of the sepals, and by association of the flowers in long, almost uninterrupted groups. *Calluna vulgaris* is visited by at least as many insects as *Erica tetralix*, and by a greater variety owing to

the accessible position of the honey. While in the flowers of *Erica tetralix*, which hang vertically, great regularity prevails in the arrangement of the parts, the style occupying the axis of the flower, and the anthers forming a circle symmetrically round it with their orifices directed downwards, in the flowers of *Calluna*, which are almost horizontal, insects are liable to be dusted with pollen from above, as the style and stamens curve upwards and permit the insect to reach the honey only by way of the lower half of the flower.

The larger bees, such as hive-bees and humble-bees, clinging with forelegs and midlegs to the outer side of the flower, weigh it down into the vertical position; then, hanging on below, they suck the honey and dust themselves with pollen, which would be sprinkled on them just as well and just in the same manner if the

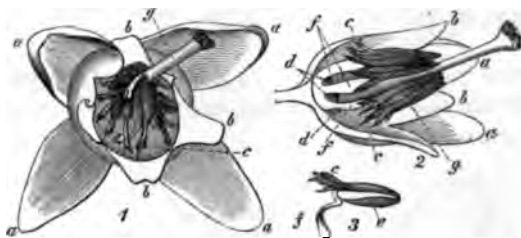


FIG. 124.—*Calluna vulgaris*, L.

1.—Old flower, seen from almost straight in front.

2.—Younger flower, after removal of half of the calyx and corolla.

3.—A stamen.

a, sepal; b, corolla; c, appendages of anthers; d, nectaries; e, anther-orifice; f, filament; g, style.

style and stamens were central as in *E. tetralix*. But the smaller bees and flies thrust head or proboscis from the front into the flower, and the upward curvature of the style and stamens causes the insect to enter by the lower half of the flower, and so to get dusted with pollen from above.

As the bud opens, the anthers dehisce, and their appendages, which are set with squarrose hairs, diverge so far outwards that they cannot fail to be touched by the proboscis of any insect-visitor, and then, as the shock is communicated to the anthers, the pollen is shaken out. The style, which even in the bud overtops the stamens, grows very markedly after the flower opens, as the flower itself does (cf. 1 and 2, Fig. 124). As a rule, it attains its full length only after the anthers have completely shed their pollen, at which time also the four-lobed stigma reaches its full development; but

the stigma, even when the flower first opens, is capable of causing pollen-grains to adhere to it, and is not rarely found dusted with pollen at that period. Thus cross-fertilisation is insured rather by the position of the stigma in advance of the anthers than, as Severin Axell supposes, by proterandrous dichogamy. Self-fertilisation does not occur.

A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, very ab., sucking only; (2) *Bombus terrestris*, L. ♀ ♂, s. (as late as Oct. 14); (3) *Diphysis serratulæ*, Pz. ♀, s.; (4) *Saropoda bimaculata*, Pz. ♀, s., with pollen of *Calluna* among its collecting-hairs; (5) *Andrena fulvicrus*, K. ♀, s.; (6) *A. fuscipes*, K. ♀ ♂, s.; (7) *A. dorsata*, K. ♀; (8) *A. parvula*, K. ♀; (9) *A. simillima*, Sm. ♀ ♂, the last three s. and c.p.; (b) *Vespidæ*: (10) *Vespa holsatica*, F. ♀, s. B. Diptera—*Syrphidæ*: (11) *Chrysotoxum octomaculatum*, Curt.; (12) *Melithreptus scriptus*, L.; (13) *Syritta pipiens*, L.; (14) *Serico-myia borealis*, Fallen (Thuringia); (15) *Cheilosia scutellata*, Fallen; (16) *Syrphus* sp., all sucking. C. Thysanoptera—(17) Numerous species of Thrips. See also No. 590, III.

Treviranus' general assertion (742) that *Ericaceæ* fertilise themselves before the flower opens needs no further contradiction after the foregoing examples.

#### Tribe *Rhodoreæ*.

*Loiseleuria (Azalea) procumbens*, L.—While the higher passes of the Alps are still covered with snow under the hot June sun, the projecting hillocks are carpeted with the red or crimson flowers of *Loiseleuria*. Numerous flies, humble-bees, and Lepidoptera fly from one tuft to another over the snow in search of honey, and as the flowers are proterogynous, cross-fertilisation takes place regularly (609).<sup>1</sup>

*Kalmia*.—The striking peculiarity of this genus,—viz. that the anthers are held fast in pouches of the corolla, until an insect-visitor touches the elastic, outwardly-bent filaments, setting them free and letting them return to their erect position,—was described in the case of *K. latifolia*, L., (*K. polifolia*, Wngnham.) by Sprengel, but was explained by him as a contrivance for self-fertilisation. Dr. Hasskarl seems even to suppose that this beautiful mechanism simply serves for spontaneous self-fertilisation; for he says nothing about the action of insects, and declares that the stamens release themselves spontaneously and effect self-fertilisation (313).

<sup>1</sup> In *Die Alpenblumen* the figure of this flower has been accidentally assigned to *Empetrum nigrum* (fig. 67).

Delpino and Hildebrand on the contrary, point out rightly that the floral mechanism of *Kalmia* leads to cross-fertilisation in case of insect-visits; they both maintain, in opposition to Hasskarl, that in *K. latifolia* the anthers cannot spontaneously release themselves from their pouches. According to Delpino, the filaments are sticky at the base in this species, so that they cling to an insect which has inserted its head into the flower, and are pulled up by it when it leaves (178, 360).

The fertilisation of *K. angustifolia* and *K. latifolia* by the hive-bee and other Hymenoptera, had been observed and described two years

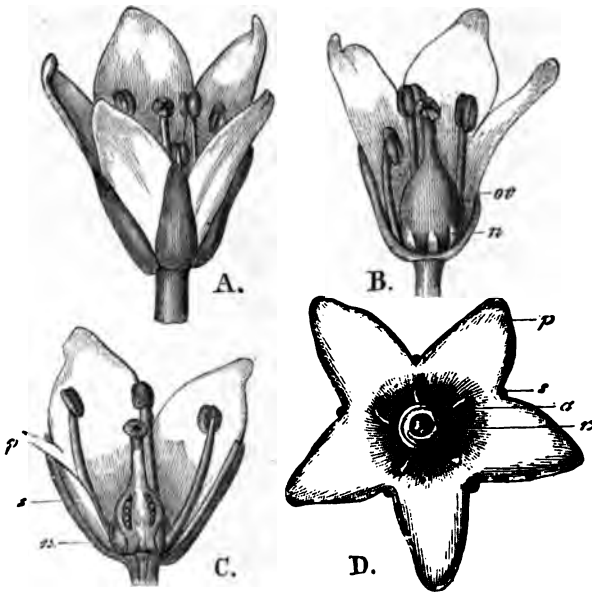


FIG. 125.—*Loiseleuria procumbens*, L.

- A.—Young flower, viewed obliquely from above. The stigma is mature, the anthers still closed.  
 B.—Ditto, in section.  
 C.—A slightly older flower, in section. The stigma is mature, the anthers have dehiscent.  
 D.—Still older flower, from above. The stigma is withered, the anthers are still covered with pollen.  
 (Fluella, Alpenrose, June 22, 23, 1879).

before by Professor W. J. Beal. The insect alights on the style, and turning round upon it, applies its proboscis successively to the outer sides of the filaments to obtain the honey which is secreted there abundantly. In doing so, it sets free the stamens with its legs, and generally receives the charge of pollen upon its body. If insects are excluded from the plant by means of a net, the flowers wither and fall off without the stamens being set free.

Only here and there are anthers found to have escaped from their pouches (Professor W. J. Beal, No. 41, and J. T. Rothrock, No. 676).

*Rhododendron ferrugineum*, L., was found by Ricca to be proterandrous, and visited by humble-bees at a height of over 7,000 feet (665). The position of the honey causes an insect-visitor to pass towards it by way of the upper half of the horizontal flower, and as the stamens and style curve upwards, they come in contact with the ventral surface of the insect. In the first stage the style is shorter than the stamens and the stigma is immature; the anthers dehisce apically by means of two orifices. Afterwards when the pollen has usually been all carried away, the style elongates to its full length and the stigma attains its full development; but the latter is still slightly overtopped and almost touched by the tallest anthers, and in absence of insects it must frequently come in contact with the pollen. Whether such self-fertilisation is effective is unknown (609).

*Rhododendron Rhodoræ*, Don. (*Rhodora canadensis*, L.)—The floral mechanism is described by Hildebrand (367).

#### Tribe *Pyroleæ*.

*Pyrola uniflora*, L., and *P. rotundifolia*, L.—These species are probably cross-fertilised by short-lipped insects, which may be seen applying their mouths to the moist stigma and the orifices of the anthers. I have directly observed cross-fertilisation performed in this way in the case of *Pyrola minor*, L. (No. 609, figs. 149, 150).

Eugene Warming found flowers of different forms and sizes on *P. minor*. He observed a plentiful secretion of honey in the case of *P. secunda* (762).

#### ORD. EPACRIDÆÆ.

*Epacris*.—Delpino found one species to be proterogynous (178).

#### ORD. PLUMBAGINÆÆ.

Some Brazilian species of *Plumbago* and *Statice* are dimorphic, according to Fritz Müller (550).

*Armeria*, according to Treviranus, is self-fertilising. As the anthers dehisce, the filaments curve inwards, bringing the anthers immediately above the depressed centre of the stigma on which they shed their pollen (742).

## ORD. PRIMULACEÆ.

The species of *Primula* have been the subject of a series of interesting researches since Darwin first led the way. In his paper "*On the two forms or dimorphic condition in the species of Primula, and on their remarkable sexual relations*" (No. 154), he showed that in *P. veris* the stigma in the long-styled form possesses papillæ three times as long as those of the short-styled form; and that the pollen-grains of the long stamens are half as large again as those of the short; that the same holds good of *P. Auricula* and *P. sinensis*; that these *Primulas* are very unproductive in absence of insects,<sup>1</sup> but fully productive when artificially fertilised or when insects have access to them; and that in artificial fertilisation legitimate<sup>2</sup> crossings gave a yield half as great again as illegitimate.

Hildebrand repeated Darwin's experiments on *P. sinensis*, and obtained almost identical results. He performed the additional experiment of fertilising flowers of each kind with their own pollen, and found that this was the least productive of all ways. Also Hildebrand sowed the seeds which resulted from the various modes of fertilisation, and showed that the union of two long-styled flowers produced mainly long-styled plants, and the union of two short-styled flowers produced mainly short-styled plants; while legitimate crossing of the two kinds of flowers produced offspring consisting of both forms in tolerably equal numbers (No. 340, 1864).

Treviranus had already (No. 742, 1863), added *P. farinosa*, *P. villosa*, and *P. minima* to Darwin's list of dimorphic species. Mr. John Scott (No. 692, 1864) enumerated altogether thirty-six species of *Primula* as dimorphic, and six as homomorphic, and showed that *P. mollis* was homomorphic and regularly self-fertilised, *P. scotica* homomorphic, but rarely self-fertilised, though fruitful to its own pollen, *P. verticillata* homomorphic, and usually unproductive when fertilised with its own pollen.

Axell figures the homomorphic and proterandrous flowers of *P. stricta*, and states that they fertilise themselves (17).

Ricca describes *P. longiflora*, All., as homomorphic and proter-

<sup>1</sup> Darwin found that, in absence of insects, the long-styled form of *P. sinensis* was twenty-four times as productive as the short-styled. Hildebrand found both absolutely barren.

<sup>2</sup> i.e. the fertilisation of either form with pollen from the other form.

androus, the style being long and exerted, and the anthers standing in the mouth of the long tube (665).

Darwin compared the productiveness of legitimate and illegitimate crossings in *Primula veris*, *P. elatior*, Jacq., *P. vulgaris*, *P. sinensis*; Hildebrand in *P. sinensis* and *P. Auricula*; Scott in *P. sikkimensis*, *P. cortusioides*, *P. involucrata*, and *P. farinosa* (167).

According to Darwin, the common Oxlip is a natural hybrid between the primrose and cowslip, while the Bardfield Oxlip (*P. elatior*, Jacq.) is a good (heterostyled) species (161, 167).

288. *PRIMULA ELATIOR*, Jacq.—Honey is secreted by the base of the ovary. In the short-styled flowers the tube is 15 to 17 mm. long, and begins to widen at a height of 12 to 13 mm.; the stigma stands in the middle of the tube and the anthers in the wide entrance. In the long-styled form the tube is 12 to 14 mm. long, and begins to widen out at a height of 4 to 5 mm.; in the middle of the tube, at the base of the expanded portion stand the anthers, and the stigma stands at or a little above the mouth of the tube. Humble-bees can insert their heads (5 mm. long) wholly into the tube, and so require a proboscis at least 12 mm. long to extract the honey from the longest flowers, and one at least 7 mm. long to do so in the shortest. As in *Pulmonaria*, the bee, if it gains the honey in the ordinary manner and not by biting a hole through the tube, must touch the organs which stand in the mouth of the flower with its head, and those in the middle of the tube with its maxillæ; and so, passing from flower to flower, it effects legitimate cross-fertilisation. Pollen-collecting bees are only able to secure their pollen in the short-styled flowers; they learn to recognise the long-styled plants at a distance and to avoid them, and then never perform cross-fertilisation but very often self-fertilisation.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus hortorum*, L. ♀ ♂ (18—21), sucking normally, s. and c.p., very ab.; (2) *B. silvarum*, L. ♀ (12—14), sucking normally; (3) *B. lapidarius*, L. ♀ (12—14), do.; (4) *B. confusus*, Schenck, ♀ (12—14), do.; (5) *B. terrestris*, L. (7—9), makes a hole in the corolla-tube, a little above the calyx, sometimes biting it with its mandibles, sometimes piercing it with its maxillæ, and so reaching the honey with its tongue (I have sometimes seen this bee, before boring the flower, make several attempts to reach the honey in the legitimate way,—this observation is of interest, as proving that the bee is not guided by instinct to the plant adapted for it, but that it makes experiments, and gets its honey where and how it can); (6) *Osmia rufa*, L. ♂ (7—8); (7) *Apis mellifica*, L. ♀, I saw both of these species thrust their tongues into several flowers, and then abandon the plant; (8)

*Anthophora pilipes*, F. ♀ ♂ (19—21), sucking normally and c.p., very ab.; (9) *Andrena Gwynana*, K. ♀ (24), c.p. on the short-styled form, ab. It holds the anthers in the mouth of the flower with its forefeet, bites the pollen loose with its mandibles and sweeps it with the tarsal brushes of the midlegs into the collecting-hairs of the hindlegs. It visits the long-styled form also, but flies away immediately; not, however, without performing cross-fertilisation in the momentary visit. I have never seen a pollen-collecting humble-bee alight on a long-styled flower; it seems to recognise them at some distance and to avoid them. B. Diptera—*Bombylidae*: (10) *Bombylius discolor*, Mgn. (11—12), s., ab.; (11) *B. major*, L. (10), much less freq., probably in most cases unable to reach the honey. C. Coleoptera—*Staphylinidae*: (12) *Omalium florale*, Pk., ab., creeping about in the flowers. See also No. 590, III.



FIG. 126.—*Primula integrifolia*, L.

- A.—Short-styled, B.—Long-styled plant (nat. size).  
 C.—Short-styled, D.—Long-styled flower in section (nat. size).  
 E.—Stigmatic papillae of short-styled flower.  
 F, G.—Ditto of long-styled flower.  
 H.—Stigma of short-styled flower, I.—Ditto of long-styled flower ( $\times 7$ ).  
 K.—Moistened pollen of short-styled flower, L.—Ditto of long-styled flower.

*Primula officinalis*, Jacq. (*P. veris*, L.), the Cowslip.—The structure of the flower resembles that of *P. elatior*; the visitors include humble-bees and *Anthophora pilipes* (509, III.).

The handsome red Alpine species, *Primula integrifolia*, L., *villosa*, Jacq., *farinosa*, L., *viscosa*, All., *minima*, L., *longiflora*, All.,

are all adapted for *Lepidoptera* by their colour and by the narrowing of the mouth of the tube.

All these species, with the exception of *P. longiflora*, are heterostyled (609).

*Primula farinosa* occurs both on the Alps and in North Germany, and probably owes this wide distribution to the mild climate succeeding the Glacial period. On the Alps, where it is visited by *Lepidoptera* in great numbers (I have noted forty-eight species), the entrance of the flower is distinctly narrower than in North Germany, where *Lepidoptera* are less plentiful and where the plant has probably to depend on the visits of bees (609).

*Primula longiflora* is homostylic, and adapted by its long narrow tube for *Lepidoptera*. The tube is 16 to 24 mm. long, and the honey is, therefore, accessible only to *Macroglossa stellatarum* (25 to 28) and to *Deilephila euphorbiæ* (25 mm.) among all the Alpine *Lepidoptera*.

289. *HOTTONIA PALUSTRIS*, L.—The flowers are dimorphic. Honey is secreted by the ovary. In both kinds of flowers, the tube

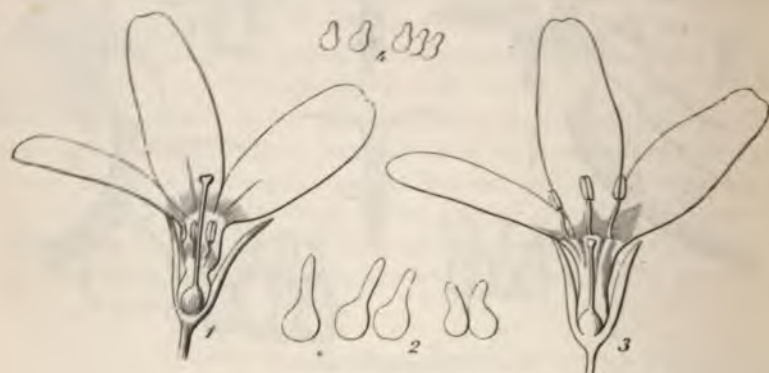


FIG. 127.—*Hottonia palustris*, L.

- 1.—Long-styled flower.
- 2.—Its stigmatic papillæ.
- 3.—Short-styled flower
- 4.—Its stigmatic papillæ, on the same scale as 2.

is 4 to 5 mm. long, the organs of one sex standing in its entrance and those of the other projecting 3 to 4 mm. beyond. In the damp state the pollen-grains of the long-styled form (which in legitimate crossing have to traverse a style 4 to 5 mm. long) are spherules  $\cdot 011$  to  $\cdot 014$  mm. in diameter; those of the short-styled

form (which in legitimate fertilisation traverse a style 7 to 9 mm. long) are spherules  $\cdot 018$  to  $\cdot 023$  mm. in diameter.

The stigma in the long-styled form, which has to receive the larger pollen-grains, may be seen with a simple lens to be rough and velvety; its papillæ are very much larger than those on the stigma in the short-styled form, which appears fairly smooth under a lens (cf. Fig. 127, 1, 2).

Insects in sucking the honey touch organs of equal height with the same parts of their bodies, and so effect legitimate cross-fertilisation regularly. Pollen-seeking insects have no need to thrust their heads into the flower in the short-styled form, and hence do not come in contact with its stigma; they come in contact with the stigma in long-styled flowers, into which they have to thrust their heads to reach the pollen. In visiting several long-styled flowers consecutively they must as a rule bring about illegitimate crossing. Probably the much greater productiveness of illegitimate crossings in the case of long-styled than in short-styled flowers (vide next table) is due to the fact that the former kind of illegitimate crossings occur frequently in nature while the latter do not, and that the former alone, therefore, are of use in reproducing the plant.

Visitors: A. Hymenoptera—*Sphegide*: (1) *Pompilus viaticus*, L., s., thrusting its head into the tube. B. Diptera—(a) *Empide*: (2) *Empis livida*, L.; (3) *E. leucoptera*, Mgn.; (4) *E. pennipes*, L., all three ab., s.; (b) *Syrphide*: (5) *Eristalis arbustorum*, L.; (6) *E. nemorum*, L., both freq., s. or f.p.; (7) *Rhingia rostrata*, L., s., ab. Five additional visitors (*Diptera*) are enumerated in No. 590, III.

Sprengel was aware of the dimorphism of this plant, and suspected that it had some unknown purpose. *Hottonia palustris* occurs with cleistogamic flowers (167).

Mr. John Scott performed on *Hottonia palustris* the same experiments that Darwin had first instituted on *Primula*, and obtained likewise the result that legitimate or heteromorphic crossings are the most productive (692).

In the summer of 1867, I repeated Scott's experiments on specimens which I kept in a large vessel of water in my room, with the following results:—

form (which in legitimate fertilization is univerted a style 7 to 9 mm long) are spherules 0.18 to 0.28 mm in diameter.

The stigma in the long-styled form which has to receive the larger pollen-grains, may be seen with a simple lens to be rough and velvety; its papillae are very much larger than those on the stigma in the short-styled form which appears fairly smooth under a lens (cf. Fig. 127, 1, 2).

Insects in sucking the honey must remain of equal height with the same parts of their bodies, and so effect legitimate cross fertilisation regularly. Pollen-seeking insects have no need to thrust their heads into the flower in the short-styled form, and hence do not come in contact with its stigma; they come in contact with the stigma in long-styled flowers, into which they have to thrust their heads to reach the pollen. In visiting several long-styled flowers consecutively they must as a rule bring about illegitimate crossing. Probably the much greater productiveness of illegitimate crossings in the case of long-styled than in short-styled flowers (vide next table) is due to the fact that the former kind of illegitimate crossings occur frequently in nature while the latter do not, and that the former alone therefore are of use in reproducing the plant.

[illegible]

Sprengel was aware of the significance of this fact and suspected that it had some unknown purpose. *Stemmatopus* occurs with cleistogamic flowers.

**Mr. John Scott** performed as *Holloway* from the first  
institute on January 1st,  
last or before.

	Flowers which were artificially fertilised.	Flowers, by the pollen of which the flowers were fertilised.	Number of capsules.	Number of seeds.	Average num- ber of seeds in a capsule.	Number of weighed seeds.	Total weight of seeds in milligrammes.	Average weight of a single seed in milligrammes
A.—LEGITIMATE CROSSINGS.								
1a.*	Long-styled ...	Short-styled ...	14	1323	94.8	1323	104	0.078
b.*	—	—	20	1786	89.3			
2a.	Short-styled ...	Long-styled ...	14	861	61.5	861	34.7	0.040
b.	—	—	6	632	105.3	632	27.8	0.043
c.	—	—	10	495	49.5			
B.—ILLEGITIMATE CROSSINGS OF SEPARATE PLANTS.								
3a.	Long-styled ...	Long-styled ...	11	764	69.4	764	58.7	0.076
b.	—	—	7	632	90.3	532	33.7	0.063
4a.	Short-styled ...	Short-styled ...	7	118	17.8	118	15.1	0.117
b.	—	—	12	233	19.8	133	17.9	0.129
C.—CROSSINGS BETWEEN FLOWERS OF THE SAME PLANT.								
5.	Long-styled ...	Long-styled ...	An unfortunate accident spoilt the results.					
6a.	Short-styled ...	Short-styled ...	15	134	9			
b.	—	—	17	5	0.3			
D.—STIGMA FERTILISED WITH POLLEN OF THE SAME FLOWER.								
7a.	Long-styled ...	Long-styled ...	11	226	20.5			
b.	—	—	16	199 (38 very small.)	12			
8a.	Short-styled ...	Short-styled ...	13	68	5.2	68	9.6	0.141
b.	—	—	17	128	7.5			

\* a, b, c, indicate different individual plants.

Although these observations are in some places defective, they illustrate well on the whole Darwin's law that in heterostyled plants legitimate crossings are the most fruitful.

Also the preceding table shows clearly that self-fertilisation and the crossing of flowers on the same plant are much less productive even than illegitimate crossings of flowers on different plants. And of very special interest is the fact, brought out by my experiments, that in *Hottonia palustris* illegitimate crossing between different plants of the long-styled form is just as productive as the legitimate crossings are.<sup>1</sup>

I have shown above that this kind of illegitimate crossing is to a great extent performed by pollen-feeding flies. If we suppose that the superior effect of legitimate crossing in other dimorphic and trimorphic plants results from their being exclusively or almost exclusively fertilised legitimately in a state of nature, and that other ways of fertilisation from long disuse may and do become

<sup>1</sup> This result is arrived at by comparing 1b and 2b in the foregoing table; if, on the other hand, as Darwin rightly insists (No. 167, chap. i.), we add the number of seeds from all the capsules produced by the two modes of fertilisation, we obtain as the mean number in the long-styled capsules, after legitimate fertilisation, 91.4, after illegitimate, 77.5, or in the proportion of 100 to 85.

inoperative, we can easily comprehend how in *Hottonia palustris* application of pollen from a long-styled flower to a long-styled stigma on another plant has retained its full efficiency.<sup>1</sup>

*Androsace Vitaliana*, K.S., is dimorphic (Treviranus, No. 742; Darwin, No. 167).

The Alpine species of *Androsace* (*A. septentrionalis*, L., *A. Chamæjasme*, Host., *A. obtusifolia*, All., etc.) are homogamic, and visited chiefly by Diptera, but to some extent by Lepidoptera and small bees; in absence of insects they are self-fertilised (No. 609, figs. 140, 141).

Species of *Cortusa* fertilise themselves, according to Treviranus, by the style bending back towards the anthers (742).

*Dionysia*, Fenzl., is dimorphic according to Kuhn (399).

The Alpine species of *Soldanella* are adapted for bees by the pendulous or inclined bell-shaped flower, the lilac or violet colour, the position of the anthers close around the style, and the more or less complete protection of the honey from small insects by means of the anthers and appendages of the corolla (609, figs. 146-148).

290. *LYSIMACHIA VULGARIS*, L.—The following varieties of this plant occur near Lippstadt: (a) on sunny embankments, a conspicuous form which is never or only rarely self-fertilised; (b) in shady hollows, a less conspicuous form which fertilises itself regularly; (c) transition forms in spots intermediate in character, e.g. on the banks of ditches exposed to the sun. In the form (a) the petals are dark-yellow, red at the base, recurved, expanding widely, about 12 mm. long and 6 mm. broad on an average, and the filaments are red near the end; the style projects several millimetres beyond the tallest anthers, so that in case of insect-visits, cross-fertilisation takes place regularly, but in absence of insects, self-fertilisation cannot easily occur. In (b) the petals are light-yellow and of one colour throughout, 10 mm. long and 5 mm. broad on an average, not spreading out so widely, but for the most part diverging obliquely upwards; the filaments are greenish-yellow; the style is of the same length as the two inferior and longer stamens, so that in absence of insects self-fertilisation always occurs. (c) The intermediate forms differ from (b) either (1) by the

<sup>1</sup> This reasoning, however, is directly opposed to other cases, such as that of *Linum grandiflorum*, in which the long-styled form is quite unproductive with pollen from another long-styled flower, although from the position of the anthers it is regularly conveyed to the stigma (No. 167, chap. vi.).

red colour of the filaments, or (2) by the larger size of the petals, or (3) in both characters together, or in addition (4) by a slight red colouring in the base of the corolla, or still further (5) by a slight extension of the style beyond the longer stamens. All such intermediate stages between the extreme forms occur in the same localities, and not unfrequently even on the same plant.

These forms of *Lysimachia vulgaris* form another illustration of the law, exemplified in so many previous cases, that while it is of advantage to the plant when sure of insect-visits to be capable of cross-fertilisation only, it is above all important that, where insect-visits are rare, the plant shall be capable of reproducing itself by self-fertilisation.

I have not discovered honey in any of the forms of this plant. The flowers are visited regularly and persistently by pollen-seeking insects, and sometimes by honey-seeking insects which fly away after a few vain attempts to find honey.

A. Hymenoptera—(a) *Apidae*: (1) *Macropis labiata*, Pz. ♀ ♂, rather ab., especially the females, on the sunshine-loving form of the plant. I found the females as a rule only on flowers of this plant, diligently sweeping the flowers and piling large masses of moistened pollen on their hind legs. I am still unable to decide where they got the material to moisten the pollen with. I should suppose that they bored into the succulent tissue of the flower, were it not that the mandibles are blunt and fringed at the end: perhaps the sharp points at the end of the short blunt tongue do this work, which usually belongs to the mandibles. (2) *Halictus zonulus*, Sm. ♂, scarce; (3) *Andrena denticulata*, K. ♂, scarce; (b) *Vespidae*: (4) *Odynerus parietum*, L. ♀, scarce (the last three had obviously visited the flower in the vain hope of honey). B. Diptera—*Syrphidae*: (5) *Syritta pipiens*, L., f.p. on the self-fertilised shade-loving form; (6) *Syrphus balteatus*, Deg., f.p.

*Lysimachia nummularia*, L., is almost always sterile (Darwin, No. 158), perhaps because all the examples in the same neighbourhood come from the same stock (cf. Eug. Warming, No. 762).

*Lysimachia thyrsoflora*, L., is proterogynous (762).

*Centunculus minimus*, L., is regularly self-fertilised, according to Ascherson (10); it could hardly be otherwise, to judge from the inconspicuousness of the flowers.

*Anagallis arvensis*, L., and *A. cærulea*, Schreb.—Delpino is of opinion that *A. cærulea* and *arvensis* were originally two forms of a single dimorphic species, which became independent ("divorzio di due forme riunite originariamente sopra una pianta dimorpha;" No. 172, p. 45); but as yet this view is without proof.

The flowers of both species are adapted for insects in a simple and effective way, so that cross-fertilisation in case of insect-visits and self-fertilisation in absence of insects are equally well insured. During the sunniest hours of the day, from about 9 A.M. to 3 P.M., the petals (scarlet in *A. arvensis*, blue in *A. cœrulea*), which cohere only by a ring at the base, spread out almost to a vertical plane, which has a diameter of 10 to 12 mm. in *A. arvensis* and rather less in *A. cœrulea*; the five stamens protrude from the centre of the flower, and the style projects between the stamens and curves downwards, so that an insect alighting on the lower part of the corolla and going towards the anthers comes first in contact with the stigma. Stigma and anthers ripen simultaneously; the pollen,



FIG. 128.

1, 2.—*Anagallis arvensis*, L.

1.—Fully expanded.

2.—Half closed.

3, 4.—*A. cœrulea*, Schreb.

3.—Fully expanded.

4.—In section. ( $\times 8\frac{1}{2}$ .)

st, stigma.

which coats the anthers all round, is all that the flowers offer to insect-visitors, unless perhaps the delicate red, jointed, knobbed hairs which clothe the filaments are manipulated by flies with their labellæ, as I have observed in the case of the hairs upon the filaments of *Verbascum*.<sup>1</sup> In either case it is to the stamens that insects come, and if they alight on the interior part of the flower as the most convenient place for them, the downward curvature of the stigma suffices to insure cross-fertilisation. About 3 P.M. the sepals and petals begin to close up, so that the coloured surface formed by the corolla is reduced to less than a fourth of its former

<sup>1</sup> According to Delpino, *Anagallis* and also *Verbascum* are adapted for pollen-collecting bees, which cling to the staminal hairs; but as to *Anagallis* direct observation is yet wanting (No. 178, II. p. 296).

size (cf. Fig. 128, 1 and 2). The plant, therefore, no longer attracts insects, but by the closure of the flower the stigma is drawn inwards and brought in contact with the three inferior anthers; so that self-fertilisation results, unless insects have been attracted during the warm hours of the day and have removed the pollen from the anthers, at the same time cross-fertilising the stigma.

I have not yet observed insects visiting either species.

*Trientalis europæa*, L., is proterogynous and devoid of honey (590, III.).

#### ORD. EBENACEÆ.

*Diospyros virginiana*, L., according to Asa Gray, is probably androdicæcious (167, 2nd ed.).

#### ORD. OLEACEÆ.

Species of *Jasminum* are self-fertilised, according to Treviranus (742), the style curving back towards the anthers. Kuhn mentions *Jasminum* as containing dimorphic species (399).

*Forsythia* is heterostyled (Darwin, No. 167), but not invariably so (590, III.).

291. *SYRINGA VULGARIS*, L.—Honey is secreted by the ovary, and occupies 2 to 4 mm. of the tube, which is 8 to 10 mm. long;

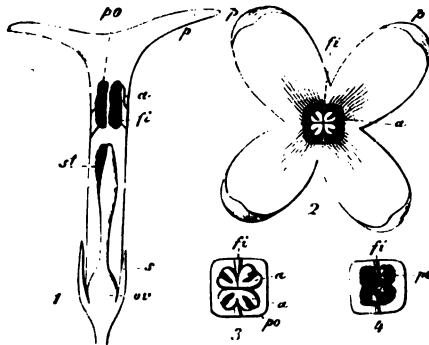


FIG. 129.—*Syringa vulgaris*, L.

- 1.—Flower, from the side, after removal of half the corolla.
  - 2.—Ditto, from above.
  - 3.—Mouth of the flower, immediately after its expansion.
  - 4.—Ditto, somewhat later.
- s, sepal; p, petal; fi, filament; a, anther; po, pollen; ov, ovary; st, stigma.

it is sheltered from rain by the two stamens, which to a great extent fill up the mouth of the tube, and the length of the tube

protects it from short-lipped insects: it is all the more diligently sought therefore by insects whose proboscis is sufficiently long. An insect in inserting its proboscis brings it in contact first with the anthers, which stand in the mouth of the tube, and then with the stigma, which is lower down: stigma and anthers are matured simultaneously. If a smooth, dry needle be thrust into the flower, it may readily be seen that as it enters no pollen sticks to it, and as it is withdrawn pollen only adheres to it for 2 to 4 mm. at the end, where it is moist with honey. The same thing doubtless takes place in the case of honey-sucking insects, which must therefore perform cross-fertilisation regularly; while pollen-feeding insects can scarcely ever effect cross-fertilisation, but must often cause the loosened pollen to fall upon the stigma and lead to self-fertilisation. In absence of insects, self-fertilisation always occurs ultimately.

According to Batalin (38), there are two cultivated varieties—one proterandrous, the other proterogynous. I have only once seen the proterandrous variety; all the plants on which I made my observations were homogamic.

Sprengel never observed insects on this plant.

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Bombus lapidarius*, L. ♂ ♀ (10—14), ab.; (2) *B. terrestris*, L. ♂ ♀ (7—9); (3) *B. hortorum*, L. ♀ ♂ (18—21), very ab.; (4) *Apis mellifica*, L. ♀ (6), ab.; all sucking. (To judge from the length of its proboscis, the honey-bee can obtain only part of the honey); (5) *Eucera longicornis*, L. ♂ (10—12); (6) *Anthophora pilipes*, F. ♀ ♂ (19—21), ab.; (7) *Osmia rufa*, L. ♀ (7—9), ab., the three last sucking; (8) *Halictus albipes*, F. ♀; (b) *Vespidae*: (9) *Odynerus* sp.; the two last seek in vain for honey. B. Diptera—(a) *Bombylidae*: (10) *Bombylius major*, L. (10), s.; (b) *Syrphidae*: (11) *Rhingia rostrata*, L. (11—12), very ab., s. and f.p.; (12) *Xylota segnis*, L., f.p., after seeking in vain for honey; (13) *Syritta pipiens*, L. (3), f.p.; (14) *Eristalis sepulchralis*, L., f.p.; (15) *E. arbustorum*, L. (4—5), f.p. C. Lepidoptera—(a) *Rhopalocera*: (16) *Papilio Machaon*, L. (18); (17) *P. Podalirius*, L.; both ab. (Stromberg); (18) *Vanessa urticae*, L. (12), ab.; (19) *Pieris cardamines*, L. (11); (20) *P. brassicae*, L. (15); (21) *P. napi*, L.; (22) *P. rapae*, L.; all three ab.; (b) *Sphinges*: (23) *Macroglossa fuciformis*, L., freq. (Stromberg); (24) *M. stellatarum*, L., do.

*Syringa persica*, L., is gynomonœcious (605).

292. *LIGUSTRUM VULGARE*, L.—Honey is secreted by the ovary, and lies at the base of the tube, which is scarcely 3 mm. long and expands above into a four-lobed, rarely five-lobed, limb. The more or less distinctly bilobed stigma is situated at the mouth of the tube. The two (rarely three) stamens are matured simul-

taneously with the stigma, and project from the tube; the anthers dehisce laterally, but so widely, that the whole of their inner faces are covered with pollen. The two anthers stand sometimes wide apart (Fig. 130, 4), at other times they bend inwards over the stigma (1, 2); in the former case, an insect's proboscis in entering the flower first touches with one side an anther, and immediately afterwards the stigma with the opposite side, and so passing from flower to flower leads to cross-fertilisation; in the latter case self-fertilisation and cross-fertilisation may result indifferently. Insect-visits are very scarce by day; perhaps the



FIG. 130.—*Ligustrum vulgare*, L.

- 1.—Flower, seen obliquely from above.  
 2.—Ditto, not so far advanced, seen directly from above.  
 3, 4.—Flowers, seen from the side, after removal of half the corolla ( $\times 3\frac{1}{2}$ ).

white, sweet-scented flowers attract nocturnal Lepidoptera in greater numbers. Flowers whose anthers are inclined inwards above the stigma always fertilise themselves in absence of insects.

A. Hymenoptera—*Apidae*: (1) *Heriades truncorum*, L., s. (June 27, 1869).  
 B. Diptera—*Syrphidae*: (2) *Eristalis nemorum*, L., s. (June 21, 1868). A further list of visitors (four beetles, two flies, two bees, seven Lepidoptera) is given in No. 590, III.

#### ORD. APOCYNACEÆ.

293. *VINCA MINOR*, L.—The structure of the flower was correctly described by Sprengel, but incorrectly explained, since he overlooked here, as elsewhere, the advantage of cross-fertilisation. Sprengel had found *Thrips*, but no other insect, in the flower, and he supposed that in creeping in and out of the flower it transferred pollen to the stigma of the same flower, and that in this way alone fertilisation was effected.

Darwin (153) gave the first correct account of the mechanism of *Vinca*, for he recognised that a long thin proboscis in passing into the flower gets smeared with adhesive matter, and

in being drawn out carries with it pollen, which in the next flower is left attached to the stigmatic edge of the disk which terminates the style. And in the case of *Vinca major*, which Darwin had never seen visited by insects in England nor bearing fruit, he obtained good seed by repeatedly passing a fine bristle down among the stamens in six flowers on two plants, and thus effecting both cross- and self-fertilisation. Another English observer (122A) was led by Darwin's account to perform the same experiment on *Vinca rosea*, L.; he obtained good seed, though he had before found the plant always unproductive. A third English observer (636A) maintained that he had got good seed from *Vinca rosea* when left to itself. But Darwin showed that this last

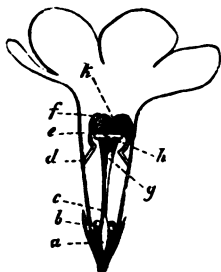


FIG. 131.—*Vinca minor*, L.

Flower, after removal of the anterior part of the corolla.

a, ovary; bb, two yellow honey-glands at the base of the ovary; c, style; d, point where the filaments separate from the corolla, marked externally by depressions; d, e, filament with its inward bend; e, f, anther, dehiscing introrsely; g, thickening of the style; h, disk-shaped end of the style, surrounded with viscid matter and functioning as a stigma on two sides of its lower edge; k, hairs upon the stigma-disk which receive the pollen as it issues from the anthers.

result was faulty, as the plant stood in a greenhouse with open windows, by which moths might enter (153, p. 831).

Delpino, unaware of these observations, gave later a full account, agreeing with Darwin's, of the mechanism of the flower of *Vinca*; his description was taken from *V. rosea*, in which the lower border of the stigmatic disk extends downwards in the form of an inverted cup (173, pp. 15-17). Hildebrand afterwards gave figures of the flowers, which illustrated Delpino's account (352).

None of the foregoing observers seem to have seen any insects except *Thrips* on any species of *Vinca*, which is remarkable, as *V. minor* in its season (beginning of April until May) is most conspicuous and rich in honey, and in my experience is in sunny weather visited abundantly by insects. The tube of the corolla is 11 mm. long in *V. minor*, but insects can easily insert their heads

into the upper part until the way is barred immediately above the anthers by hairs; the two yellow nectaries lying beside the ovary are distant only 8 mm. from this point.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus hortorum*, L. ♀ (21); (2) *B. lapidarius*, L. ♀ (12—14); (3) *B. agrorum*, F. ♀ (12—15); all three very ab. (4) *B. terrestris*, L. ♀ (7—9), less ab.; (5) *B. vestalis*, Fourc. ♀ (12), scarce; (6) *Anthophora pilipes*, F. ♀ ♂ (19—21), very ab.; (7) *Osmia rufa*, L. ♂ (7—8). B. Diptera—*Bombylidæ*: (8) *Bombylius major*, L. (10); (9) *B. discolor*, Mik. (11—12), very ab., the latter species (April 18, 1869) as early as 7.45 A.M. All the visitors sucking normally. C. Thysanoptera—(10) *Thrips*, ab. See also No. 590, III.

294. *VINCA MAJOR*, L.—I have once seen *Bombus agrorum*, F. ♀ (12—15 mm.), visiting this plant; it sucked numerous flowers, thrusting its head completely into the mouth of the tube.

*Tabernæmontana echinata*, Aubl., is barren when fertilised with pollen of the same flower or of other flowers on the same plant, and is productive only when fertilised with pollen from another plant (Fritz Müller, No. 359).

*Apocynum androsæmifolium*, L., is fertilised by butterflies, and cements its pollen to the insect's tongue (Ludwig, No. 432).

*Apocynum hypericifolium*, Ait., has the same arrangement (Ludwig, No. 443).

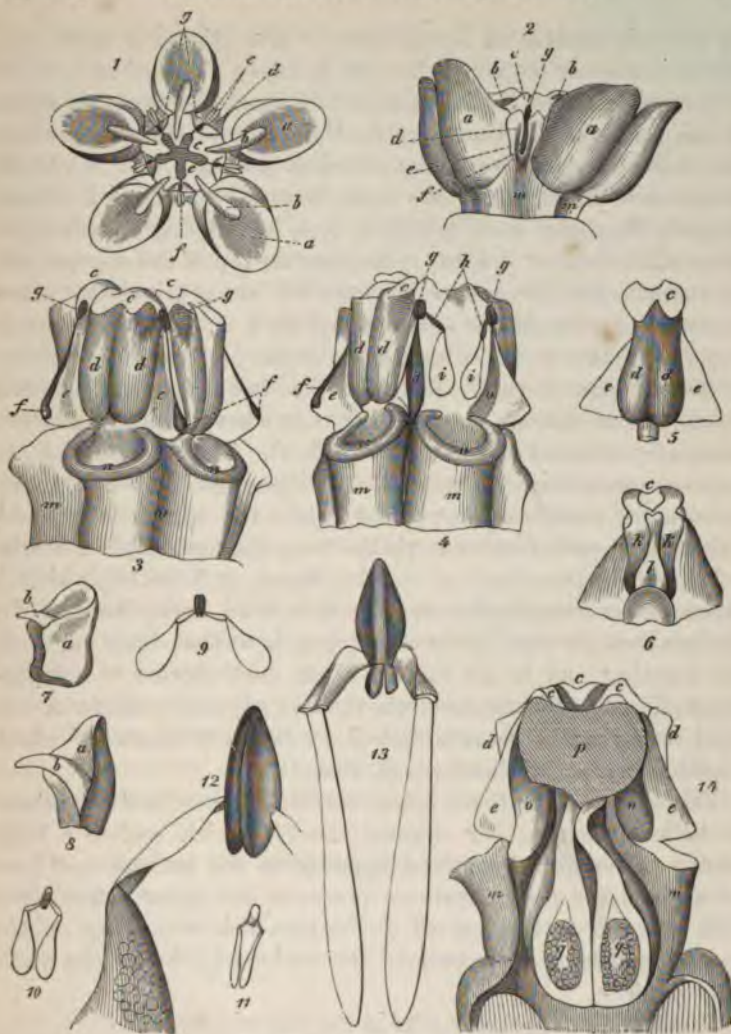
*Nerium Oleander*, L., and *N. odorum*, Ait., are adapted for long-tongued Lepidoptera (443).

In *Rhynchodia* (*Rhynchospermum*) *jasminoides*, according to Hildebrand, as in *Vinca*, the insect's proboscis is smeared with adhesive matter as it enters, and cemented to the pollen as it is withdrawn (No. 356, p. 509).

#### ORD. ASCLEPIADEÆ.

295. *ASCLEPIAS CORNUTI*, Dec. (*A. syriaca*, L.).—The *Asclepiadææ* rival the Orchids, if not in the variety of their forms, at least in their complexity and in their perfect adaptation to insect-visitors. Hildebrand has so thoroughly described the way in which *A. Cornuti* is fertilised by insects (347), that I have scarcely anything new to add to his description; yet it may be well that I should illustrate the complex mechanism by figures, and catalogue the insects that effect fertilisation.

The two ovaries (*q*, 14) are surrounded by a fleshy column (*m*, 14, 2, 3, 4) and covered by a thick, fleshy disk (*p*, 14), and

FIG. 132.—*Asclepias Cornuti*, Dec.

- 1.—Flower, after removal of sepals and petals, viewed from above ( $\times 34$ ).
  - 2.—Ditto, from the side.
  - 3.—Ditto, after removal of the cuculli ( $\times 7$ ).
  - 4.—Ditto, after removal of one anther.
  - 5.—The anther removed from Fig. 4, outer view.
  - 6.—Ditto, inner view.
  - 7.—A cucullus, from the side ( $\times 34$ ).
  - 8.—Ditto, in section.
  - 9.—Pollinia, immediately after extraction, outer view ( $\times 7$ ).
  - 10.—Ditto, when the twisting of the retinacula is half completed.
  - 11.—Ditto, twisting complete.
  - 12.—Corpusculum and retinacula more magnified, outer view.
  - 13.—Ditto, inner view.
  - 14.—Section of flower, after removal of sepals, petals, and cuculli.
- a, cucullus; b, its conical process; c, upper membranous process of anther; d, outside of anther-loculus; e, anther-wing; f, slit between two adjacent anther-wings; g, corpusculum; h, retinaculum; i, pollinium; k, k, empty loculi of anther; l, connective; m, column; n, place of attachment of a cucullus; o, stigmatic chamber; p, fleshy stigma-disk; q, ovary.

they are only capable of fecundation at five stigmatic spots close beneath the lower border of the disk (*o*, 14, 4). The column, which really consists of the united staminal filaments, bears at its upper end five anthers. The anthers lie close around the stigma-disk; each of them lodges two flattened pollen-masses (*i*, 4, 9, 10, 11) in two pouches (*k*, 6), which are open internally, and are indicated externally by slight swellings (*d*, *d*, 3, 4, 5). A thin membranous process of the anther (*e*, 5, 14) rests upon the top of the stigma-disk, and on each side the anther is produced into a triangular membranous expansion (ala or anther-wing) (*e*, 3, 5, 14), which stands out perpendicular to the column close to the corresponding process of the adjacent anther. Between the two adjacent processes of each pair of anthers, there is left only a very narrow slit which is distinctly wider at its lower end (*f*, 3, 4). The slit leads into an elongated space which we may call the stigmatic chamber (*o*, 4, 14); for about the middle of its vertical height the stigma is exposed. At the upper end of the slit, visible from the outside, is a bright, black body (*corpusculum*) of regular shape (*g*, 1 to 14), which is seen on closer examination to be a thin, hard, horny lamina. Its sides are bent forward for its whole length so that their edges lie close together, and in the middle of its lower border is a wedge-shaped slit. To this *corpusculum* the two adjacent pollinia of two neighbouring anthers are attached by bands (*retinacula*)<sup>1</sup> which lie hidden beneath the anthers (*h*, 4, 9, 13).

The upper end of the column carries, besides the five anthers, five hollow, fleshy, foliar organs (*cuculli*), which secrete a large quantity of honey; they stand opposite to the anthers, and from each an incurved pointed process proceeds, the upper extremity of which rests upon the top of the stigma-disk, and lying on the superior membranous process of the anthers (*c*) keeps the whole firmly in place.

This singular apparatus acts in the following way:—

Insects (bees, wasps, flies) which creep about the umbels in search of honey, attracted by the sweet scent of the flowers, slip upon the smooth parts of the flower until a foot enters the wide inferior part of a slit, in which at last it gets a firm hold. When the insect tries to draw its foot out in order to proceed further, the diverging claws are caught by the apposed edges of the anther-wings, and guided upwards in the slit, so that one or other of the two claws is brought without fail into the notch in the lower border of the *corpusculum* and there held fast. If the insect now

<sup>1</sup> These structures are not in any sense homologous with the *retinacula* of Orchids.

draws its foot forcibly out, it brings with it the corpusculum (*g*) and the two pollinia (*i*) attached to it by their retinacula (*h*). The pollinia stand wide apart when they are extracted (*9*); but the retinacula twist inwards as they dry (cf. 9, 10, 11) bringing the pollinia so close together that they may easily be introduced into another slit. As the insect moves on over the umbel, its foot bearing the pollinia slips into the lower part of a slit of another flower; and this time as the leg is drawn up the pollinia are left in the stigmatic chamber opposite to the stigma, since the slit is too narrow to admit of their further passage upwards; and the insect, freeing its foot by a violent pull snaps the retinacula and so extricates itself. The pollinia are left behind in the stigmatic chamber, while the corpusculum and its broken retinacula are carried off still firmly attached to the insect's foot. The insect continues its visits, and the retinacula attached to its feet now get fixed in corpuscula as the claws did before, and an insect's foot after repeated visits may sometimes be seen bearing many corpuscula with their retinacula, often dichotomously arranged.

Delpino saw *A. Cornuti* in Florence fertilised in the manner which I have described by *Scolia hortorum*, *S. bicincta*, *Apis mellifica*, and *Bombus italicus* (172, 352).

I have observed many bees, wasps, ants, and flies, on the flowers of *A. Cornuti* in Thuringia. Dr. Hildebrand sent me a still larger number of insects with corpuscula on their claws, which he had caught on this plant at Freiburg in the first hot days of July, 1870.

The following list comprises the insects observed by Delpino, Hildebrand, and myself:—

(Fl. = Florence, *Delpino*; F. = Freiburg, *Hildebrand*; Th. = Thuringia, *H. Müller*; ! = with corpuscula on their claws).

A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀! (Fl., Th.); (2) *Bombus italicus*, L. ! (Fl.); (3) *B. terrestris*, L. ♂ ♂! (F.); (4) *B. hypnorum*, L. ♀! (F.); (5) *Halictus Scabiosæ*, Ill. ♀! (F.); (6) *H. cylindricus*, F. ♂! (F.); (7) *H. quadricinctus*, F. ♀! (F.); (8) Several small species of *Halictus* (Th.), which I never saw caught in the slits; (9) *Cœlioxya* sp. ♀ ♂! (F.); (10) *Stelis aterrima*, Pz. ♀! (F.); (b) *Sphegidae*: (11) *Scolia hortorum*, L. ! (Fl.); (12) *Sc. bicincta*! (Fl.); (13) *Sc. quadripunctata*, F. ♀! (F.); (14) *Ammodia sabulosa*, L. ♀! (F.); (15) *Psammophila affinis*, K. ♀! (F.); (c) *Vespidæ*: (16) *Polistes gallica*, L. ♀! (F., Th.), and var. *diadema*! (Th.); (d) *Formicidæ*: (17) Various species (Th.); they got caught in the slits and were not able to set themselves free. I have never seen an ant tear its leg off in order to escape. B. Diptera—(a) *Syrphidæ*: (18) *Eristalis tenax*, L. ! (F., Th.); (19) *E. arbustorum*, L. ! (Th.); (20) *E. nemorum*, L. ! (Th.); (21) *Melithreptus scriptus*, L. (Th.);

(22) *M. tæniatus*, Mgn. (Th.); both of these obtained the honey without getting caught in the alits. (b) *Muscidæ*: (23) *Ocyptera brassicaria*, F. (F.); (24) *Lucilia* (Th.) In several flowers which I dissected, the corpuscula and pollen masses were still in their places, though pollinia, which must have come from other flowers, had been inserted into the stigmatic chambers.

The following additional list is taken from my *Weitere Beobachtungen*, III. p. 61. The insects were for the most part observed in my garden in July.

A. Diptera—*Empidæ*: *Empis livida*, L., s. ! B. Hymenoptera—*Apidæ*: *Bombus muscorum*, L. (*B. agrorum*, F.) ♂, s. ! ab., Würzburg; *Cœlioxya conoidea*, Ill., ♀ ♂ ! ab. C. Lepidoptera—*Noctuidæ*: *Hypena proboscidalis* L., s., not extracting the pollinia; *Plusia gamma*, L., do., in the evening; *Sphingidæ*: *Sesia formiciformis*, Esp. ♂ (*teste* Speyer), do. D. Neuroptera: *Panorpa communis*, L., s. and extracting the pollinia.

*Asclepias curassavica*, L., according to Fritz Müller's observations in South Brazil, is sometimes visited by wasps, but infinitely more frequently by a great variety of butterflies, on whose legs the corpuscula and pollinia of this plant may often be found. One

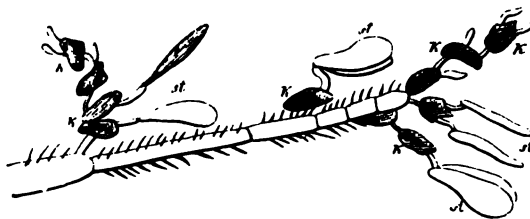


FIG. 133.

Butterfly's foot, bearing eleven corpuscula (k) and eight pollinia (st) of *Asclepias curassavica*, L.

butterfly, like a *Vanessa*, bore on one leg no less than eleven corpuscula of this *Asclepias*. Eight only of the twenty-two pollinia remained, the others had been employed in the fertilisation of other flowers.

*Asclepias tenuifolia* (?) was seen by Hildebrand to be fertilised by a cabbage-white butterfly (361).

*Gomphocarpus (Asclepias) fruticosa*, R. Br.—The structure of the flower and the way in which insects visit it have been described by Sprengel (No. 702, pp. 139-150): he fell into the error of considering the upper surface of the stigma-disk to be the stigma.

*Araujia albens*, Brot. (*Physianthus*, Mart.), is fertilised by humble-bees, to whose tongues the corpuscula become attached.

*Vincetoxicum officinale*, L., is fertilised by the proboscides of small flies, *Stapelia hirsuta*, L., and *S. grandiflora*, Mass., by *Musca vomitoria* and *Sarcophaga carnaria*, which are attracted by the putrid odour of the flowers. As a rule, in those Asclepiadæ in which fertilisation is effected by an insect's proboscis (*Araujia*, *Cynanchum*, *Vincetoxicum*, *Stapelia*, *Boucerosia*), the five nectaries alternate with the stamens; in those in which fertilisation is effected by the legs of insects (*Asclepias*, *Gomphocarpus*, *Centrostemma*, *Hoya*), the reverse holds; in *Stephanotis*, which is fertilised by the proboscides of nocturnal Lepidoptera, the base of the tube of the corolla forms a large honey-receptacle (172, 352).

In *Ceropejia elegans*, Wall., the flower forms a temporary prison for its visitors, very much like that of *Aristolochia Clematidis*, L. Small flies (*Gymnopa opaca*) creep through the tube of the flower, which is at first erect, into the expanded portion which surrounds the reproductive organs; in this expanded portion, or cage, whose entrance is surrounded by stiff hairs pointing inwards, they are imprisoned for a whole day. On the second day these hairs wither, the flower bends over, the flies creep out with the pollinia attached to their proboscides, and seek new flowers, in whose cages they introduce the pollinia into the slits leading to the stigma, and get new pollinia attached to their proboscides (178, 360).

*Cynanchum Vincetoxicum*, R. Br.—The flower agrees in most points with that of *Asclepias Cornuti*.

The dirty-white flowers of *Cynanchum*, devoid of the pleasant perfume of *Asclepias*, are adapted for fertilisation by carrion-loving flies, which convey the exceedingly minute pollinia, not with their claws, but with the bristles on their proboscides. Further, while in *Asclepias Cornuti* the foliar appendages of the anthers form five fleshy cups filled with honey alternating with the corpuscula, here the same appendages of the anthers form high vaulted fleshy bodies coherent into a ring; and alternating with them are five deep nectariferous pits immediately below the five corpuscula. Into these pits, insects thrust their proboscides, to suck the nectar. When *Muscide* (in which the proboscis is set with erect bristles) do this, it is almost inevitable that when the proboscis is being drawn back, one or other of its bristles gets caught in the slit, which is placed over the nectary and is wider below than above; after entering the slit, it glides upwards between the lateral anther-wings of the two neighbouring anthers, straight into the inferior wedge-shaped notch of the corpusculum, and is there held fast. When the fly now gives a slight pull backwards in order to free

papillar inner surfaces are exposed to contact with the bee. So if bees visit the flower, cross-fertilisation seems to be insured; in absence of insects, self-fertilisation seems to be rendered impossible by the well-marked proterandry, and by the position of the anthers in regard to the ripe stigmas. I have only noticed humble-bees visiting the plant: viz. (1) *Bombus agrorum*, F. ♀ (12—15); (2) *B. senilis*, Sm. ♀ (14—15), both very frequent, sucking honey only.

*Gentiana ciliata*, L., is proterandrous, and adapted for humble-bees. Honey is secreted by yellow fleshy areas of the base of the corolla between each pair of stamens (No. 609, fig. 132).

*Gentiana bavarica*, L., and *G. verna*, L., are adapted for cross-fertilisation by Lepidoptera. The most important visitor seems to be *Macroglossa stellatarum* (No. 570, vol. xv.; No. 609, fig. 131).

*G. nivalis*, L.—The flower resembles the two preceding species in structure, but is less conspicuous and less visited by insects; in case of need it fertilises itself (570, 609).

297. *GENTIANA AMARELLA*, L.—Honey is secreted by five green fleshy spots at the base of the corolla, alternating with the stamens; it is sheltered from rain by the closing of the flower during dull weather, and is protected from flies by long, erect hairs developed on the interior of the corolla at the junction of its tube and limb. The plant grows among grass, and accordingly the lobes of the erect corolla spread out to be mainly conspicuous from above.

The tube is 16 to 18 mm. long, but as it is 6 mm. wide at the mouth a humble-bee can insert the whole of its head and reach the honey with a proboscis 10 to 12 mm. long. Unlike *G. Pneumonanthe*, the flowers are homogamous. When the flower opens the anthers dehisce, after turning their dehiscent sides, which in the young bud were turned outwards, upwards so as to be touched the more certainly by the bee's head. The two terminal lobes of the style are already expanded and provided with stigmatic papillæ. In case of insect-visits, self-fertilisation is not impossible; but since the stigma stands above the anthers, the insect as a rule comes in contact with it first, and effects cross-fertilisation. After the pollen is shed the anthers again come to lie in a line with the filaments and place themselves close round the style. I have not observed whether self-fertilisation occurs in absence of insects. I have seen *Bombus silvarum*, L. ♀ (12—14), visiting the plant, and sucking numerous flowers (Sept. 30, 1869).

*Gentiana tenella*, Rottb. (*G. glacialis*, Thom.), *G. nana*, Wulf.,

*G. campestris*, L., and *G. obtusifolia*, Willd., are adapted for fertilisation by humble-bees and Lepidoptera in the same way as *G. Amarella*, L. (No. 570, vol. xv.; No. 609, figs. 133-135).

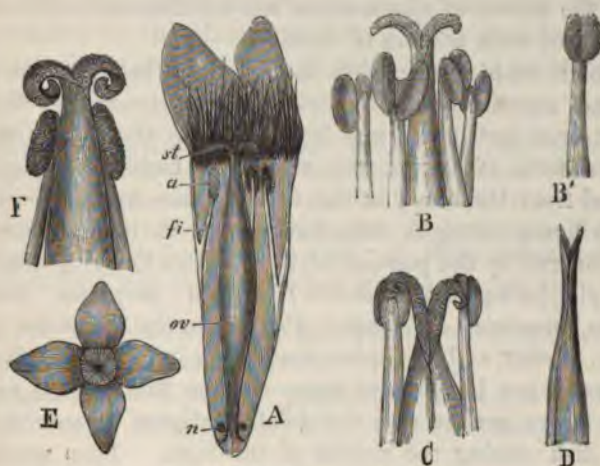


FIG 135.—*Gentiana campestris*, L.

- A.—An old flower. The calyx and nearly half of the corolla have been removed.  
 B.—Essential organs from a flower in the act of opening. The stigma is mature, the anthers are still closed; but they dehiscent while I was drawing them (B').  
 C.—Upper part of the pistil and of two opposite stamens, in their natural position: from a somewhat older flower.  
 D.—Stigma, whose branches have closed up after being dusted with pollen ( $\times 7$ ). (Madulein June 20, 1879.)  
 E.—A flower viewed directly from above (natural size).  
 F.—Upper part of the pistil and of two stamens in their natural position: from still older flower ( $\times 7$ ).  
 (Albula, August 20, 1878).

*G. obtusifolia* is proterandrous, *G. tenella* and *G. nana* homogamous, *G. campestris* sometimes homogamous, sometimes slightly proterogynous.

#### REVIEW OF THE GENUS GENTIANA.

A comparison of the very numerous Alpine Gentians suggests the following theory of their evolution.

The genus *Gentiana* splits into two main divisions, in one of which honey is secreted by the base of the ovary, in the other by the base of the corolla.

We have an offshoot of the first main division in *G. lutea*, which stands on a much lower grade than the other species and nearer to the primitive form. The ancestors of the genus undoubtedly had, like *G. lutea*, fully open flowers with almost free

petals, and offered their insect-visitors either honey lying fully exposed in the angle between ovary and corolla, or pollen only. In either case the most various insects were admitted, and they performed cross-fertilisation (as in *G. lutea*) casually and irregularly, so that the power of spontaneous self-fertilisation could no more be dispensed with than in *G. lutea*.

In both main divisions, as the nectaries became more perfect, bees and especially humble-bees proved themselves the most efficient cross-fertilisers; and in relation to their visits the campanulate form of flower was evolved. Unbidden guests were excluded from the honey in the first division by the development of deep honey-passages, cross-fertilisation in case of bees' visits being insured by the position of the anthers in a ring close round the style (sub-genus *Calanthe*; species *purpurea*, *pannonica*, *punctata*, *cruciata*, *aslepiadea*, *Pneumonanthe*, *Fralichii*, *frigida*, *acaulis*). Later, as Lepidoptera made their influence felt, the corolla in *Calanthe* got longer and narrower, the folds which narrow it became more perfect, and the bilobed stigma became developed into a disk closing the mouth of the tube. Thus resulted the Alpine sub-genus *Cyclostigma*, adapted for long-tongued Lepidoptera (species *bavarica*, *verna*, *æstiva*, *imbricata*, *pumila*, *utriculosa*, *nivalis*).

In the second division, hairs on the corolla afforded imperfect protection against unbidden guests, and narrowing of the corolla made it more certain that both stigma and anthers should be touched by the bee (sub-genus *Crossopetalum*; species *ciliata*, L.). And finally, in a special offshoot of this division, as Lepidoptera here also came to have a decided influence as cross-fertilisers, the fringe of hairs at the mouth of the corolla became more developed, excluding all visitors except humble-bees and Lepidoptera from the honey, and the corolla became so narrow that Lepidoptera as well as humble-bees must perform cross-fertilisation in inserting their proboscides (sub-genus *Endotricha*; species *campestris*, *germanica*, *Amarella*, *obtusifolia*, *tenella*, *nana*).

The primitive yellow colour, retained in *G. lutea*, was gradually exchanged for blue by the influence of the humble-bees, and instructive transition-stages in this process are preserved among the species of *Calanthe*.<sup>1</sup> But after the blue colour was once firmly established it was retained throughout the changes by which *Calanthe* passed into *Cyclostigma* (609).

<sup>1</sup> *C. punctata* has only blue spots on the pale-yellow ground of the corolla; and in *C. purpurea*, the outside of the corolla is bluish-purple, but the inside is still yellow.

298. *ERYTHRÆA CENTAURIUM*, L.—I, like Sprengel, have failed to find any honey in this flower, though I have seen it repeatedly visited by Lepidoptera, and though the spiral twisting of the stamens (like the twisting of the stigma in several *Sileneæ* fertilised by Lepidoptera) seems to be an adaptation to insure their being touched by the thin proboscis of these insects. Probably the insect pierces some soft tissue with the sharp points at the tip of its proboscis.

Visitors: Lepidoptera—(a) *Sphinxes*: On July 10, 1868, in Thuringia, I saw *Macroglossa stellatarum*, L., sucking first on *Dianthus Carthusianorum* and then on *E. Centaurium*; (b) *Noctuæ*: On Sept. 1, 1871, at Lippstadt, my son Hermann saw (2) *Plusia gamma*, L., and (3) *Agrotis pronuba*, L., freq. sucking persistently on flowers of this plant. An additional list, including five Lepidoptera, three bees, and one *Empis*, is given in No. 590, III.

Mr. A. S. Wilson found this plant heterostyled and with dimorphic pollen-grains (780).

*Limnanthemum* (Kuhn, No. 399) and *Villarsia* (= *Limnanthemum Humboldtianum*, Fritz Müller, No. 550) are dimorphic (Darwin, No. 167, p. 116).

*Menyanthes trifoliata*, L., is well known to be dimorphic. In a small marsh near Lippstadt, sometimes flooded by the Lippe, which probably brought the seeds, I have found the long-styled form only; and I have never observed ripe fruit there.

#### ORD. POLEMONIACEÆ.

*Cobæa penduliflora* is fertilised by Sphingidæ (226), *C. scandens*, Cav., by humble-bees (52).

*Collomia grandiflora* (Dougl.), Lindl., has cleistogamic flowers (423, 424, 685).

299. *PHLOX PANICULATA*, L.—Sprengel recognised the proterandrous condition of this flower, and found it to be visited by butterflies. I have seen *Conops flavipes*, L., sucking honey, and *Eristalis tenax*, L., very frequently eating pollen on the flowers.

*Polemonium cæruleum*, L., is likewise proterandrous. Sprengel overlooked the dichogamous condition in this plant, but Axell (17) figures the proterandrous flowers.<sup>1</sup>

The honey is secreted in this species and in *Phlox paniculata* by the lower fleshy part of the ovary.

<sup>1</sup> See also my *Alpenblumen*, pp. 257-259, fig. 97, and *Weitere Beobachtungen*, III. pp. 8, 9.

Treviranus supposed that *Polemoniaceæ* fertilise themselves before the flowers open (742).

*Gilia pulchella*, Dougl., and *G. (Leptosiphon) micrantha*, Steud., are believed by Darwin (167) to be heterostyled.

Professor Asa Gray considers *Phlox subulata*, L., to be heterostyled, but Darwin (167) shows that the great variability of the stigmas and pollen-grains makes this a perplexing case. He says,

Possibly this species was once heterostyled, but is now becoming sub-dicæcious, the short-styled plants having been rendered more feminine in nature." (*Forms of Flowers*, p. 121.)

#### ORD. BORAGINÆÆ.

##### Tribe *Cordiææ*.

*Cordia*, L., is heterostyled, but the stamens are of almost the same length and the pollen-grains are of the same size in the flowers of both forms (Darwin, 167).

##### Tribe *Boragææ*.

300. SYMPHYTUM OFFICINALE, L.—A white, annular ridge at the base of the ovary secretes honey, which is lodged in the upper part of the inverted corolla. The whole corolla is 14 mm., its upper narrower portion 8 mm., long. The long, trihedral invaginations of the corolla, which pass from the boundary between the wide and narrow parts into the wide part of the bell, closing in the spaces between the stamens, were thought by Sprengel to guard the nectar from rain; but as in the preceding species, this service is performed by the inverted position of the corolla. Their use is probably to cause an insect to thrust its proboscis between the closely approximated anthers, and not into the wide intervals between the stamens. The sharp teeth which these appendages of the corolla bear aid in this object; they certainly do not act as "pathfinders," as Sprengel thought, for to an insect inserting its head into the flower from below, they appear not bright and shining, as Sprengel describes them, but as dark points, guarding all but the legitimate access to the honey. This view is confirmed by a comparison of the lengths of the proboscides of insects which reach the honey of this flower in the normal way, and of those which do so by biting a hole in the narrow part of the corolla. To reach the honey by passing between the anthers an insect requires a proboscis at least 11 mm. long; to reach it by passing between

the filaments from the interior of the corolla would require a proboscis only 8 mm. long. Now I have found the following insects always sucking normally on this flower: *Rhingia rostrata*, L. (11—12); *Bombus silvarum*, L. ♀ ♂ (11—14); *B. agrorum*, F. ♀ (13—15); *B. Rajellus*, Ill. ♀ ♂ (11—13); *Anthophora pilipes*, F. ♀ (20—21); the following, on the other hand, only reach the honey from outside by boring a hole in the narrow part of the corolla: *B. terrestris*, L. ♀ (7—9); small workers of *B. lapidarius*, L. (9—10); and *B. pratorum*, L. ♂ (8—9). It is plain from these measurements that, had the path between the filaments remained unguarded, the three last-named insects might all have made use of it, without resorting to the slower process of piercing the corolla, and there can be no doubt that they are deterred by the sharp teeth of the corolline appendages.

The anthers, which, as in *Borago*, combine to form an inverted cone, dehisce before the flower opens; the pollen remains partly within the anthers, partly in the apex of the cone, until a humble-bee or *Rhingia* thrusts its proboscis between the anthers and lets the pollen fall out. Each pollen-grain is 0·02 mm. long, about 0·013 mm. broad, and is shaped like two spheres joined together and flattened at the junction; on being moistened with water, each pollen-grain swells into a sphere of 0·02 mm. diameter. The pollen as it falls out resolves itself for the most part into single grains, only a few of which remain adhering in groups; a considerable amount remains attached to the anther-walls until the flower withers.

The stigma ripens as soon as the flower opens, and hangs down beyond the anther-cone; an insect-visitor therefore touches the stigma before it displaces the anthers and dusts itself with pollen.

In absence of insects, self-fertilisation probably takes place.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Anthophora pilipes*, F. ♀!; (2) *Bombus agrorum*, F. ♀!; (3) *B. silvarum*, L. ♀ ♂!; (4) *B. Rajellus*, Ill. ♀ ♂!; (5) *B. terrestris*, L. ♀; (6) *B. pratorum*, L. ♂; (7) *B. lapidarius*, L. ♂, the last three gnaw through the narrow part of the tube; (8) *Eucera longicornis*, L. ♂, creeps bodily into the flower; (9) *Halictus sexnotatus*, K. ♀; (10) *Apis mellifica*, L. ♀, both suck through the holes made by humble-bees. B. Diptera—*Syrphidæ*: (11) *Rhingia rostrata*, L., s.! Only those insects marked with (!) suck normally and effect cross-fertilisation. C. Coleoptera—*Nitidulidæ*: (12) *Meligethes*. See also No. 590, III.

301. *BORAGO OFFICINALIS*, L.—The mechanism of this flower was minutely described by Sprengel, with great but not absolute accuracy. Honey is secreted by the pale-yellow, fleshy base of the ovary, and is lodged in a short tube formed by the bases of the

stamens; it is protected from rain by the inverted position of the flower. The anthers meet to form a cone; each dehiscences on its inner surface, slowly from apex to base, letting the smooth pulverulent pollen run into the apex of the cone. The style with still immature stigmas is inclosed within the cone of anthers. An insect, to reach the honey, must hang suspended below the flower, and thrust its proboscis between two stamens; two anthers are thus slightly displaced, the point of the cone opens, and a little pollen falls out.

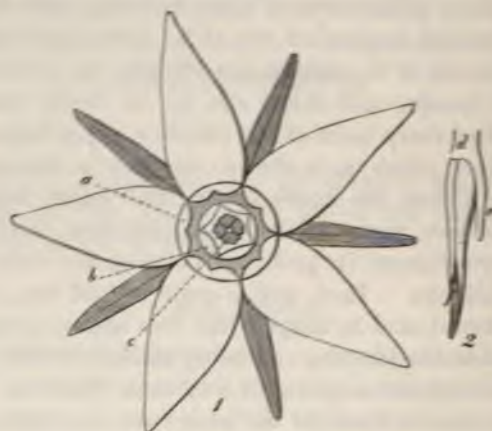


FIG. 136.—*Borago officinalis*, L.

- 1.—Flower, from below: the stamens have been cut away.  
 2.—A stamen in its natural position, viewed from the side.  
*a*, pouch in the corolla; *b*, cut end of stamen; *c*, ovary; *d*, fleshy thickened filament; *e*, process of ditto; *f*, orifice of the anther.

The pollen in each anther ripens very gradually from the apex towards the base, and hence the little shower of pollen may be emitted repeatedly. The style only grows out beyond the cone of anthers and develops its stigma, after the anthers have been emptied of their pollen. Even after repeated insect-visits a permanent displacement of the anthers cannot take place, for the short, broad form and fleshy nature of the filaments (*d*, 2), their stiff external appendages (*e*, 2),<sup>1</sup> and the invaginated processes of the corolla that surround the base of the anther-cone, insure the return of each anther to its place after every disturbance. I have neglected to observe whether finally, in absence of insects, self-fertilisation may take place.

<sup>1</sup> Sprengel thought that these appendages were for the purpose of sheltering the honey, but the inverted position of the flower renders this unnecessary. Delpino (No. 178, pp. 172-174) takes the view that I have adopted.

(1) *Apis mellifica*, L. ♀, very ab., s. and c.p.; (2) *Bombus pratorum*, L. ♀, s. and c.p.; (3) *Halictus zonulus*, Sm. ♀, s.; (4) *H. sexnotatus*, K. ♀, s., ab.; (5) *Megachile centuncularis*, L. ♂, s. See also No. 590, III.

302. *ANCHUSA OFFICINALIS*, L. (Sprengel, Pl. III., 10, 11, 16, 17).—Honey is secreted by the green fleshy base of the ovary and accumulates in the lower part of the corolla, which forms a tube 7 mm. long. The corolla is smooth within, but its entrance is guarded from rain and from unbidden guests (flies) by five closely approximated, hairy, invaginated processes. At its upper end the tube expands into a limb 10 mm. in diameter, at first concave and violet in colour, then flat and deep-blue; and further, the flowers, which are conspicuous in themselves, are rendered more so by aggregation. The invaginated appendages, which are indicated on the outside of the corolla by transverse slits, serve by their white colour as honey-guides. The anthers, which dehisce introrsely, and the stigma which overtops them, are matured simultaneously. Cross-fertilisation is insured, in case of insect-visits, by the position of the stigma; in absence of insects, self-fertilisation must finally occur, for the corolla in falling off brings the anthers in contact with the stigma.

Eug. Warming has found *A. officinalis* heterostyled, with transition-forms between the long- and short-styled flowers (762).

Insect-visits are plentiful, and in fine weather cross-fertilisation always occurs. On September 13, 1871, I observed the following insects visiting this plant on the Wandersleber Schlossberg in Thuringia:—

A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, s. and c.p., ab.; (2) *Bombus pratorum*, L. ♀, s. and c.p.; (3) *B. agrorum*, F. ♂ ♀; (4) *B. silvarum*, L. ♂; (5) *B. lapidarius*, L. ♂ ♀; (6) *B. muscorum*, F. ♀; the last four only sucking. B. Lepidoptera—*Noctuæ*: (7) *Plusia gamma*, L., very ab., s. See also No. 590, III., and No. 609.

303. *LYCOPSIS ARVENSIS*, L.—The same parts of the flower as in *Anchusa* serve to secrete, contain, shelter, and point out the honey. The flowers are doubtless visited and fertilised in like manner, chiefly by bees, and to some extent also by Lepidoptera. I have only observed (September 8, 1871, in Thuringia) *Hesperia thaumas*, Hufn., once sucking honey on this plant.

*Pulmonaria angustifolia*, L. (*P. azurea*, Besser).<sup>1</sup>—This plant is dimorphic; and the two forms of flowers, besides differences in the reproductive organs, show an unusual number of other minor

<sup>1</sup> Darwin (No. 167) has taken *P. angustifolia*, L., and *P. azurea*, Besser, to be distinct species.

differences. In the short-styled flowers, the calyx is longer and narrower, the corolla is longer and has a much larger and more conspicuous limb; the ovary is smaller; the nectaries larger and more rich in honey than in the long-styled flower. In the Alps humblebees and *Rhingia* and *Bombylius* act as cross-fertilising agents for this species, as they do for *P. officinalis* in the Lowlands (609). Hildebrand denies that this plant is heterostyled: it is possible that he made his observations on cultivated examples, and that

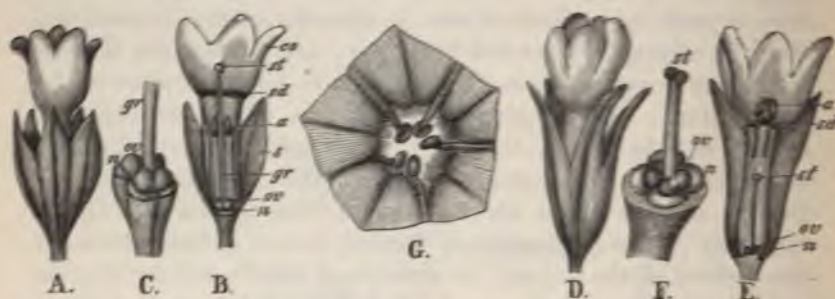


FIG. 137.—*Pulmonaria angustifolia*, L.

- A.—Long-styled flower.  
 B.—Ditto, in section.  
 C.—Ditto. *ov*, ovary; *n*, nectary; *gr*, style ( $\times 4\frac{1}{2}$ ).  
 D.—Short-styled flower.  
 E.—Ditto, in section ( $\times 1\frac{1}{2}$ ).  
 F.—Ditto ( $\times 4\frac{1}{2}$ ).  
 G.—Limb of the corolla of a short-styled flower, cut off close above the anthers, to show the protecting hairs ( $\times 4\frac{1}{2}$ ).

there is in them, as Darwin has shown in the case of *Primula sinensis*, a return to the homostylic condition (609).

Darwin found the long-styled though not the short-styled flowers of this species absolutely barren when illegitimately fertilised; he gives several reasons for considering that this dimorphic plant is in a transition-stage, tending to become diœcious (167).

304. *PULMONARIA OFFICINALIS*, L.—This species also is dimorphic. Honey is secreted by the white, basal part of the ovary, lodged in the lower portion of the tubular corolla, and sheltered from rain by a ring of hairs placed in the tube at the place where it widens out. In the short-styled flowers, the anthers stand at the mouth of the corolla (whose tube is 10 to 12 mm. long); the stigma stands half-way up the tube, on a style 5 to 6 mm. long: in the long-styled flowers these positions are reversed, the style being 10 mm. long, and the anthers, being attached by very short filaments to the corolla, 5 mm. from the base of the flower. Since the corolla widens slightly at its mouth, insects with a proboscis 8 mm.

long are able to reach the honey. Bees touch the longer reproductive organs with their heads or with the base of their proboscides, and the shorter with the maxillæ, which serve to sheath the proboscis; thus they regularly perform 'legitimate cross-fertilisation.' The flowers are very conspicuous and very rich in honey, and appear at a season when they have few rivals; they are therefore very much visited by insects, and have become sterile when fertilised with their own pollen or with pollen from another flower of the same form. Hildebrand (342) found by experiment that when he fertilised a flower of either form with its own pollen, or with pollen from another similar flower, it was completely sterile; but when fertilised with pollen from a flower of the other form, it was as productive as in the wild state. He found on investigating wild plants in fruit, that in some cases the oldest flowers on the plant, and almost constantly the terminal flowers of each shoot, bore no seed; the former fact he explains by the absence of the proper insects early in the season, the latter by imperfect nourishment of the terminal parts of the shoots.

Darwin's experiments (No. 164, p. 103) on this plant led to a result different from Hildebrand's. He found that illegitimately fertilised long-styled plants were highly fertile, producing three times as much seed as Hildebrand's wild specimens bore; and that even when self-fertilised, a few seeds were produced. Hildebrand endeavoured to explain this great discordance by the fact that the plants which he experimented on were kept in pots in the house, while Darwin's were grown out of doors.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Anthophora pilipes*, F. ♂ ♀ (19—21), very ab., s. and c.p., sucking now on *Primula elatior*, now on *Corydalis*, now on *Pulmonaria*, without restricting itself long to the same species; (2) *Bombus hortorum*, L. ♀ (21), very ab., s., and keeping to the same species of flower; (3) *B. lapidarius*, L. ♀ (12—14), s.; (4) *B. senilis*, Sm. ♀ (14—15), s.; (5) *B. agrorum*, F. ♀ (12—15), ab., s.; (6) *B. silvarum*, L. ♀ (12—14), s.; (7) *B. Rajellus*, Ill. ♀ (12—13), s.; (8) *B. terrestris*, L. ♀ (7—9), s.; (9) *B. pratorum*, L. ♀ (11—12), s., distinctly prefers *Pulmonaria*, leaving the flowers of *Primula elatior* untouched; (10) *Osmia fusca*, Christ. (bicolor, Schrank) ♀ ♂ (8), c.p. and s., ab. This species feeds itself and its young almost entirely on the honey and pollen of *Pulmonaria*. I have never found its nests (which are made in snail-shells, those of *Helix nemoralis* at Lippstadt) except where *Pulmonaria* was growing plentifully. (11) *O. pilicornis*, Sm. ♂ ♀, s. and c.p. I was the first to find this bee on the continent of Europe. I have found it exclusively on flowers of *Pulmonaria*, at Rixbeck near Lippstadt; it occurs singly among numerous examples of the foregoing species, with which it agrees in the manner of tending its young. (12) *O. rufa*, L. ♂ (7—8), s. In most of these bees I have directly observed pollen upon the maxillæ. B. Diptera—(a)

*Bombylidae*: (13) *Andrena Gwynana*, K. ♀, c.p.; (14) *Anthophora retusa*, K. ♀, c.p. and s.; (15) *Halictus cylindricus*, F. ♀, c.p.; (16) *Bombylius discolor*, Mgn. (11–12), hovers over the flower and inserts its proboscis without settling, ab., but only in warm sunshine; (17) *B. major*, L. (10), do.; (b) *Syrphidae*: (18) *Rhingia rostrata*, L. (11–12), very ab., s., but only towards the end of the flowering period (May 18, 1870). C. *Lepidoptera*—*Rhopalocera*: (19) *Rhodocera rhamni*, L., s., ab. D. *Coleoptera*—*Staphylinidae*: (20) *Omalium florale*, Pk., ab., creeping about in the flowers.

305. *MYOSOTIS SILVATICA* (Hoffm.) Lehm.—As soon as the flower opens, the anthers, which are attached to the corolla above the level of the stigma and are inclined slightly inwards, dehisce



FIG. 138.—*Myosotis silvatica*, Hoffm.

1.—Flower, from above.

2.—Ditto, in section ( $\times 7$ ).

3.—Pollen grains.

a, light-blue limb of corolla; b, white radiating bands; c, yellow centre of the corolla; d, stamen; e, stigma; f, nectary.

longitudinally, and become covered on their inner surfaces with small, white pollen-grains; each of the latter is shaped like two attached spheres, and measures  $\cdot 005$  mm. by  $\cdot 003$  mm. The stigma ripens simultaneously with the anthers. In sunny weather numerous flies frequent the flowers, which are rendered conspicuous by colour and by aggregation. The fly thrusts its proboscis rapidly into the flower, spending at most two to three seconds upon it, and probably, therefore, sucking honey in each case, not gathering pollen.

The honey is secreted by the fleshy base of the ovary, and is lodged in the lower part of the tube of the corolla, which is 2 to 3 mm. long. An insect must dip its proboscis down between the stigma and anthers, and touch them with opposite sides of the

proboscis. Since the proboscis may be inserted on any side of the stigma, the part of the proboscis dusted with pollen in one flower will very probably come in contact with the stigma in the next. Since flies often dip their proboscis repeatedly into one flower, self-fertilisation also must frequently result. In absence of insects, self-fertilisation always occurs by pollen falling directly upon the stigma. In plants which I kept in my room, guarded from insects, I always found the stigma in the older flowers thickly covered with pollen. Axell found on experiment that the plant is completely fertile when self-fertilised (17).

Delpino describes *Myosotis* as dichogamous and exclusively fertilised by bees.

*M. silvatica* in my garden is visited by the following insects:—

A. Hymenoptera—*Apidae*: (1) *Andrena albicans*, K. ♀, s. B. Diptera—(a) *Syrphidae*: (2) *Eristalis arbustorum*, L., ab.; (3) *E. sepulcralis*, L., ab.; (4) *Syrphid pipiens*, L., very ab.; (5) *Rhingia rostrata*, L.; (b) *Muscidae*: (6) *Scatophaga merdaria*, F.; (7) Species of *Echinomyia*; (8) *Onesia floralis*, R. D.; (9) *O. sepulcralis*, Mgn.; (10) *Pollenia vespillo*, F.; (11) *Musca corvina*, F.; (12) *Colobata cothurnata*, Pz.; all acting in the manner described above. A list of nineteen additional visitors is given in No. 590, III.

*Myosotis alpestris*, Schmidt.—I have observed this plant visited on the Alps by thirty-three Lepidoptera, nineteen Diptera, and one bee—a strikingly different list from the preceding one (609).

306. *MYOSOTIS INTERMEDIA*, Link. ap. Schl.—The flowers of this plant differ from those of *M. silvatica* in their smaller size, and

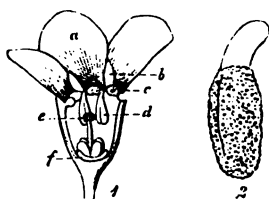


FIG. 139.—*Myosotis intermedia*, Link.

1.—Longitudinal section (× 7).

2.—Anther viewed from the side to show the broad prolongation of the connective.

in two points which make cross-fertilisation still more sure: (1) The stigma stands on a level with the anthers, so that an insect's proboscis is more certain than in *M. silvatica* to touch anthers and stigma with opposite sides, unless it be repeatedly inserted as is not

rarely the case. (2) The connective terminates above in a broad expansion, which is slightly curved outwards, but stands immediately above the anther since the latter is inclined towards the centre of the flower; this arrangement hinders the proboscis from coming in contact with the anther while being inserted. The same character is present but much less marked in *M. silvatica*.

Self-fertilisation always occurs in absence of insects.

The invaginated processes of the corolla which surround the mouth of the tube in all species of *Myosotis* serve to shelter the honey from rain, and by their yellow colour serve as "path-finders"; they also cause insects to insert their tongues in the centre of the flower and so to come more directly in contact with the stigma.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, ab., s.; (2) *Andrena fasciata*, Wesm. ♂, s.; (3) *A. albicans*, K. ♀, s. B. Diptera—(a) *Bombylidæ*: (4) *Bombylius major*, L. s.; (b) *Syrphidæ*: (5) *Chrysogaster viduata*, L., s. See also No. 590, III.

307. *MYOSOTIS PALUSTRIS*, Rth., agrees in all points with *M. intermedia*, except in the length of its tube, which is 3 mm. long.

Visitors: A. Lepidoptera—*Rhopalocera*: (1) *Lycæna icarus*, Rott., s. B. Diptera—*Empidæ*: (2) *Empis opaca*, F., very ab., s.

308. *MYOSOTIS HISPIDA*, Schlecht.—The flower is described in No. 590, III.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Halictus zonulus*, Sm. ♀, s. (Tekl. B.). B. Diptera—*Muscidæ*: (2) *Anthomyia* sp., s.

*Myosotis versicolor*, Lehm.—When the flower opens, the corolla is colourless or pale yellow, and imperfectly developed; the anthers and stigma are however ripe, and the latter protrudes a little from the flower. If insect-visits now occur, cross-fertilisation results; afterwards the corolla in elongating rubs the anthers against the knobbed stigma and the flower is self-fertilised.

I have observed bees and flies visiting the flower (570, vol. x.)

*Echinosperrum Lappula*, Lehm.—The mechanism of fertilisation resembles that of *Myosotis silvatica*, but the honey is not so accessible, as the limb of the corolla does not spread out flat, but remains bell-shaped. The corolla is white while in the bud, pale red while just emerging beyond the calyx, and afterwards bright blue. The flower is visited by Diptera, *Apidæ*, and *Sphegidæ* (590, III.; 609).

*Omphalodes verna*, Mœnch.—The tube is 3 mm. long, and the

bright blue limb of the corolla expands to a diameter of 15 to 18 mm. The connective has no terminal appendage; otherwise the flower resembles that of *Myosotis*, and self-fertilisation is likewise a regular occurrence.

Visitors: Hymenoptera—*Apidæ*: (1) *Bombus terrestris*, L. ♀, s.; (2) *Osmia rufa*, L. ♂, s.

309. *LITHOSPERMUM ARVENSE*, L.—The smooth ovary secretes a small amount of honey, which lies in the base of the corolla; the latter forms a tube 4 to 5 mm. long, and only 1 mm. wide in its lowest part. The five short stamens are inserted upon the corolla below its middle, and their anthers dehisce inwards longitudinally

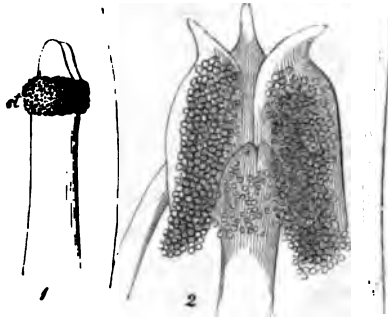


FIG. 140.—*Lithospermum arvense*, L.

1.—Tip of style, from a bud ( $\times 36$ ). st, stigma.  
2.—Position of essential organs in the flower.

and let their pollen escape, before the opening of the flower. The style, which is 2 mm. long, ends in two smooth, rounded lobes, and bears immediately below these an annular ridge covered with stigmatic papillæ; this stands on a level with the anthers, completely filling up the narrow passage to the base of the flower. The upper ends of the stamens curve slightly outwards, thus guiding an insect's proboscis to the centre of the flower and causing it to pass between the anthers and stigma. If in the young flower an insect thrusts in its proboscis, already dusted with pollen, cross-fertilisation takes place, and the proboscis gets dusted at the same time with fresh pollen. But as the pollen issues more and more from the anthers, cross-fertilisation is soon rendered more difficult, and ultimately self-fertilisation becomes unavoidable.

*Batschia* (*Lithospermum*) *longiflor*  
flowers (167).

310. *ECHIU*M *VULGARE*, L.—The  
very conspicuous, and are peculiar



FIG. 141.—*Echium vu*

- 1.—Older flower, from the side. The flower sh
  - 2.—Transverse section through the base of a fl
- k*, sepal; *bl*, corolla; *st*, stamen; *g*, style; *n*,

various sizes to perform cross-fertilis  
honey and in carrying off the pollen.

The honey, which attracts most vis  
base of the ovary, and lies in the bas

enough for large humble-bees to insert easily the head and part of the thorax, and smaller humble-bees more than half of their body; while still smaller bees can enter the tube bodily. The insect passes straight on to the base of the flower, the downward curvature of whose terminal portion corresponds to that of the insect's proboscis. To alight on the flower and suck the honey is the work of a moment; so completely is the shape of the flower adapted, not for one only, but for many species of bees. But none of the various visitors can reach the honey without getting dusted ventrally with pollen in young flowers, or leaving some of that pollen upon the stigma in older flowers. From the point where the filaments become free from the corolla, they pass on horizontally near the inferior wall of the corolla; and the four lowest stamens project some 7 mm. beyond the corolla, forming a convenient alighting-place for insects. The uppermost stamen, on leaving its attachment to the corolla, also bends downwards, and in so doing it divides the entrance to the honey-containing part of the tube into two passages; it then proceeds horizontally, but only so far as the mouth of the corolla. The free ends of all the stamens curve slightly upwards; and the anthers, which dehisce as the flower opens, turn their pollen-covered sides upwards; no bee, therefore, can alight without dusting its ventral surface with pollen. Large humble-bees bring their thorax, smaller ones their abdomen, in contact with the long stamens, while the smallest bees, which fly right into the flower, must at least come in contact ventrally with the short fifth stamen. The style lies in the midst of the stamens, and divides terminally into two short branches, which bear the stigmas at their ends. When the flower opens, the style scarcely reaches the mouth of the corolla; its distal end is straight, its two branches lie close together, and their stigmas are apparently incapable of fertilisation. In course of time the style lengthens till it projects 10 mm. beyond the mouth of the corolla; it curves gently upwards at its outer end, and its two branches, now bearing ripe stigmas, separate. The stigmas now lie above and in front of all the anthers, and no bee, large or small, can enter the flower without bringing its ventral surface in contact with them.

It is evident from the position of the stigmas that cross-fertilisation will be performed, even if pollen remains upon the anthers when the stigmas are mature.

*Echium* attracts very numerous and various insects, as the following long list shows:—

A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, very ab., s.; (2) *Bombus silvarum*, L. ♀ ♀, s. and sometimes also c.p.; (3) *B. lapidarius*, L. ♀ ♀ ♂; (4) *B. agrorum*, F. ♀ ♀; (5) *B. hortorum*, L. ♀ ♀ ♂; (6) *B. terrestris*, L. ♀ ♂; (7) *B. muscorum*, F. ♀; (8) *B. pratorum*, L. ♀; (9) *B. Rajellus*, Ill. ♀; (10) *B. hypnorum*, L. ♀; (11) *B. (Apathus) rupestris*, F. ♀; (12) *B. vestalis*, Fourc. ♀; (13) *B. campestris*, Pz. ♀ ♂; (14) *B. Barbutellus*, K. ♀; all these thirteen species of humble-bees are more or less abundant, especially the first five, all only suck, except *B. silvarum*; (15) *Anthophora quadrimaculata*, F. ♀ ♂ (Thur.), s. and c.p., ab.; (16) *A. furcata*, Pz. ♀ ♂ (Thur.), s. and c.p.; (17) *Saropoda bimaculata*, Pz. ♀ ♂, very ab., s.; (18) *Melecta luctuosa*, Scop. ♀ (Thur.); (19) *Eucera longicornis*, L. ♂; (20) *Andrena fulvicrus*, K. ♂; (21) *A. albicus*, K. ♂; (22) *A. labialis*, K. ♂; (23) *Halictus nitidus*, Schenck, ♀; (24) *H. albipes*, F. ♂; (25) *H. cylindricus*, F. ♀ ♂; (26) *H. sexnotatus*, K. ♀; Nos. 18—25 all s.; (27) *H. nitidiusculus*, K. ♀, c.p.; (28) *Nomada sexfasciata*, Pz. ♀, s.; (29) *Ceratina coerulea*, Vill. ♀, s.; (30) *Megachile Willughbiella*, K. ♂, s.; (31) *M. circumcincta*, K. ♀, s. and c.p.; (32) *Diphysis serratulæ*, Pz. ♀ ♂, s. and c.p., very ab.; (33) *Osmia fusca*, Christ. (bicolor, Schrank) ♀, s. and c.p.; (34) *O. ænea*, L. ♀ ♂, s. and c.p.; (35) *O. cæmentaria*, Gerst. ♀ ♂, c.p. and s., very abundant in Thuringia and Sauerland, building its nests in the cavities of stones, and feeding the young exclusively on honey and pollen of *Echium*; (36) *O. adunca*, Latr. ♀ ♂, very ab., also feeding its young exclusively on honey and pollen of *Echium*; (37) *O. leucomelæna*, K. ♀, c.p.; (38) *O. rufa*, L. ♀, s.; (39) *Cœlixys quadridentata*, L. (= *conica*, L.) ♀ ♂, s., ab.; (40) *C. conoidea*, Ill. (punctata, Lep.), ♀, s.; (41) *C. simplex*, Nyl. ♀, s.; (42) *C. umbrina*, Sm. ♀, s.; (43) *Chelostoma nigricorne*, Nyl. ♂ ♀, s.; (44) *Stelis phæoptera*, K. ♀, s.; (45) *St. breviscula*, N. ♂, s.; (46) *Prosopis hyalinata*, Sm. ♀, s.; (b) *Sphégidæ*: (47) *Crabro patellatus*, v. d. L. ♀ ♂; (48) *Ammophila sabulosa*, L. ♀; (49) *Psammophila affinis*, K. ♀, all three s.; (c) *Vespidæ*: (50) *Odynerus parietum*, L. ♂, s.; (d) *Chrysidæ*: (51) *Cleptes semiaurata*, F., s.; all the short-lipped Hymenoptera creep bodily into the flower to reach the honey. B. Diptera—(a) *Syrphidæ*: (52) *Rhingia rostrata*, L., s.; (53) *Helophilus trivittatus*, F., f.p.; (54) *Syrphus pyrastris*, L., f.p.; (55) *S. arcuatus*, Fall., f.p.; (56) *Melanostoma ambigua*, Fall., f.p.; (b) *Conopidæ*: (57) *Physocephala vittata*, F., s. C. Lepidoptera—(a) *Rhopalocera*: (58) *Satyrus Janira*, L.; (59) *Pieris brassicæ*, L.; (60) *Lycæna* sp.; (61) *Hesperia sylvanus*, Esp.; (62) *Colias hyale*, L. (Thur.); (63) *Melitæa cinxia*, L.; (b) *Sphinges*: (64) *Zygæna loniceræ*, Esp. (Thur.); (65) *Macroglossa stellatarum*, L.; (c) *Noctuæ*: (66) *Plusia gamma*, L., ab., all sucking. D. Coleoptera—(67) *Œdemera virescens*, L., crept far into the flower, and seemed to reach the honey. A further list of visitors in Low Germany is given in No. 590, III. A list of Alpine visitors (seventeen bees, five Lepidoptera) is given in No. 609, p. 262.

A review of this long list of insects, many of which frequent the flowers of *Echium* in great numbers, shows that the great majority come seeking honey, and only use the stamens as a landing-place. The females of bees with abdominal collecting-brushes, without any special effort, sweep up pollen with their abdominal brushes, filling them after a few visits. The flower is thus so convenient

for them that several of these bees (*Osmia adunca* and *O. cæmentaria*) resort to it exclusively, both for their own food and for that of their larvæ. *Syrphidæ* also make frequent use of the pollen, while bees with tibial or femoral collecting-baskets seldom gather it, and all other insects come solely for the sake of honey. The power of self-fertilisation has been completely lost.

This plant is gynodioecious. The female flowers differ from the hermaphrodite in having a much smaller corolla and shorter pistil; their stamens are short, and the anthers contain no sound pollen-grains (Darwin, 167).

*Cerinthæ glabra*, Mill. (*C. alpina*, Kit.).—This flower is adapted for humble-bees. Only humble-bees or other large bees can cling

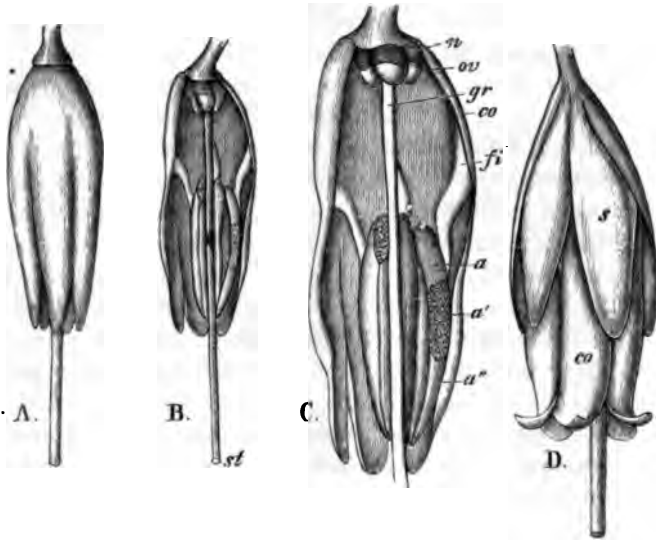


FIG. 142.—*Cerinthæ glabra*, Mill.

A.—Flower that has recently expanded.

B.—Ditto, in section ( $\times 4$ ).

C.—Older, fully expanded flower ( $\times 7$ ).

s, sepal; co, corolla; n, nectary; ov, ovary; gr, style; fl, filament.  
(Falo Alp., July 28, 1877).

to the recurved teeth of the corolla, and hanging beneath the flower, suck the honey from its base. In doing this the insect first brings its head in contact with the stigma, and then, touching the anthers with its proboscis, it dusts its head with new pollen. I have only found humble-bees (*Bombus alticola*, ♀ & ♂), but those in

(399). *Salvia* considers itself  
dimorphic, but merely show ex  
their stamens and style (167).

*Mertensia*, Roth., is dimorphi

#### REVIEW OF T

The Boragineæ have inherite  
tube which, to a certain degree, o

The lower forms (*Asperug*  
*Myosotis*) are visited and cross-  
*phidæ*), bees, and *Lepidoptera*, an  
blue colours through the selective  
in the course of individual develo  
the evolution of their colours—v  
of *Myosotis*; yellow, bluish, viole  
blue in *Pulmonaria*, *Echium*, et  
to have been the primitive colo  
violet and blue seem to have be  
tion which is 'strengthened by th  
species (*Myosotis*, *Anchusa*, *Sym*  
red varieties, apparently by rever

Starting from these simpler  
vancing adaptations for fertilisat  
by the length of its tube, protects  
of insects, excepting humble-bee

mature stigma. The drooping flowers of *Borago*, and the position of their anthers, exclude all insects which cannot hang, as bees can, below the flower and insert their proboscides into the narrow opening. *Symphytum* and *Cerinthe*, finally, besides offering the same difficulties as *Borago*, have a tube which requires so long a proboscis to reach its base, that only humble-bees and other bees with a proboscis equally long can reach the honey.

#### ORD. CONVULVULACEÆ.

311. *CONVOLVULUS ARVENSIS*, L.—Sprengel has described the chief characters of this flower very clearly, contrasting them with those of *C. sepium*.

The funnel-shaped corolla is yellow at the base internally, elsewhere either white or red, and marked in the latter case with

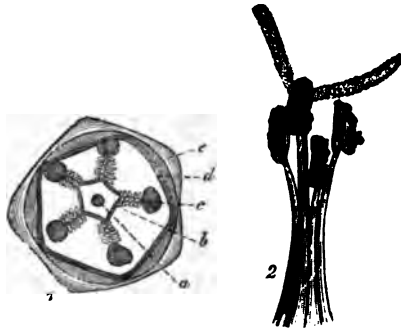


FIG. 143.—*Convolvulus arvensis*, L.

- 1.—Transverse section, through the base of the flower ( $\times 7$ ).
  - 2.—Essential organs, from an expanded flower ( $\times 8\frac{1}{2}$ ).
- a, style; b, filament; c, entrance to nectary; d, corolla; e, calyx.

five radiating white streaks. These “pathfinders,” and the habit of closing, both in the evening and in rainy weather, mark out the flower as adapted for the visits of diurnal insects. The orange-red under surface of the ovary secretes honey, which is lodged in the lowest, narrowest part of the corolla, and sheltered by the broad bases of the stamens, which leave five narrow openings leading to it. The stamens arising thus with broad bases from the corolla, adhere to it for a short distance, and then curve inwards, coming close together around the style; the filaments, where they are in contact with one another, are closely beset with small, stiff projections, which prevent an insect from thrusting its proboscis

between them. The five narrow slits between the stamens, near their base, are thus the only means of access to the honey, and the insect must make its way into the funnel between the corolla and the stamens, and then insert its proboscis into one of the slits. Since the stamens dehisce extrorsely, an insect acting in this way, unless it be too small, must be dusted with pollen; and the two branches of the stigma, standing well above the anthers, and stretching outwards over them, are touched before the anthers by the insect. In absence of insects, self-fertilisation can easily occur; for if the flower hangs down, or if the corolla withers and falls off, the pollen readily falls upon the stigma, and even in erect and fresh flowers, one of the stamens is not unfrequently seen, still covered with pollen, in contact with the stigmatic papillæ. The flowers have a peculiar aromatic smell, which seems the only reason for their being visited so much more plentifully than the larger flowers of *C. sepium*.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, very ab., s. and c.p.,—to suck, it creeps down into the base of the flower, dusting its head and back with pollen, which parts come first in contact with the stigma in each flower; (2) *Halictus morio*, F. ♂, s., touching neither stigma nor anthers; (3) *H. villosulus*, K. ♀; (4) *H. longulus*, Sm. ♀; (5) *H. nitidiusculus*, K. ♀, all three c.p.; they usually alight on the stigma and then proceed to the anthers, thus effecting cross-fertilisation; (6) *Chelostoma campanularum*, K. ♂, s., like No. 2. B. Diptera—(a) *Empidæ*: (7) *Empis livida*, L., very ab., s., thrusting its proboscis into each of the five nectaries one after another; (b) *Syrphidæ*: (8) *Helophilus florens*, L., s. and f.p.; (9) *Eristalis arbustorum*, L., s. and f.p., takes shelter from rain in the flowers; (10) *Syrphus nitidicollis*, Mgn.; (11) *S. balteatus*, Deg.; (12) *Melithreptus scriptus*, L.; (13) *M. tæniatus*, Mgn., all four f.p.,—the large honey-sucking flies effect cross-fertilisation in the same way as No. 1, the smaller pollen-feeding flies do so after the manner of Nos. 3–5; (c) *Muscidæ*: (14) *Sepsis*, abundant in the passages leading to the honey. C. Coleoptera—(a) *Nitidulidæ*: (15) *Meligethes*, do.; (b) *Ædemeridæ*: (16) *Ædemera virescens*, L., f.p.; (c) *Cerambycidæ*: (17) *Leptura livida*, L., feeding on pollen, and on the anthers. D. Hemiptera—(18) *Nabis*, s. Eighteen additional visitors are enumerated in No. 590, III.

*Calystegia sepium*, R. Br. (*Convolvulus sepium*, L.).—The flowers are scentless and without "pathfinders." In spite of their large size and conspicuous white colour, they are only scantily visited by insects. They remain open in rain. On dark evenings (between 8 and 10) I have found all the flowers closed, but all open on moonlight nights. In other respects the flowers are similar to those of *Convolvulus arvensis*. I have never observed crepuscular or nocturnal insects on the flowers, but several of my pupils have caught numbers of *Sphinx convolvuli* upon them in the

evening. In the daytime I have sometimes seen *Holictus cylindricus*, K. ♂, and *Megachile centuncularis*, L. ♂, and *Euclyptus* and *Rhingia* in special numbers, all creeping into the base of the flower, and inserting their proboscides through the slits between the filaments. *Rhingia rostrata*, L., applies its labellæ frequently to the anthers, stigma, and inner wall of the corolla, apparently picking up scattered pollen. *Meligethes*, *Thrips*, and minute *Poduræ* also frequent the flowers during the day.

Delpino mentions *Sphinx convolvuli* as a fertiliser of *C. sepium* (172, 352); he tells me by letter that one of his friends catches this insect in numbers, standing by a hedge overgrown with the plant, holding thumb and forefinger over a flower and closing its orifice when the insect has entered :

In England, where *Sphinx convolvuli* is rare, *C. sepium* seldom produces seed ; in Scotland, where *S. convolvuli* seems not to occur, *C. sepium* is rarely found wild (773). In the north of Ireland, according to Mr. T. H. Corry, *C. sepium* is far commoner than *C. arvensis*, and *Sphinx convolvuli* is comparatively frequent.

*Cuscuta Epithymum*, L., is homogamous. Honey is secreted by the lower part of the ovary, and is sheltered by scale-like appendages of the corolla. The flowers are visited by *Sphægidæ*, and in absence of insects fertilise themselves (590, III.).

*Cuscuta*, according to Kuhn, has cleistogamic flowers (399).

*Ipomæa pestigridis*, L., has cleistogamic flowers, which were known to Dillenius.

*Calonyction*, Chois.—The flowers are sterile to their own pollen.

#### ORD. SOLANACEÆ.

312. *SOLANUM TUBEROSUM*, L.—The peduncles stand almost horizontal at the time of flowering, and the five-pointed rotate limb of the corolla becomes nearly vertical. Five anthers meeting to form a cone project from the flower and surround the style, which protrudes beyond them and curves more or less downwards at its stigmatic end. All the stamens bend very slightly downwards, and the lower anthers project somewhat in advance of the others. The anthers begin to dehisce at their apex, and when touched allow a little pollen to fall out ; in some which I examined a large quantity of pollen-grains (from .013 to .021 mm. in diameter) remained in a shrivelled condition.

Since the flower secretes no honey and affords little pollen, it is very scantily visited by insects. In spite of repeated watching,

I have only occasionally seen two common Syrphidæ, *Eristalis tenax*, L., and *Syritta pipiens*, L., feeding on the pollen. Darwin observed the flower visited by humble-bees.

The stigma, from its position, must be touched by an insect-visitor before the anthers. In many flowers the end of the style curves backwards so much as to stand beneath the anthers, in the line of fall of the pollen, so that self-fertilisation may in such cases occur. Treviranus was therefore not wholly wrong when he described the genus *Solanum* as fertilised by the style curving backwards to meet the anthers (742).

313. *SOLANUM DULCAMARA*, L., is likewise devoid of honey, and is at least as scantily visited by insects as *S. tuberosum*. I have seen *Rhingia rostrata*, L., examining the greenish spots which glitter like drops of fluid in the middle of the violet corolla, and afterwards stroking the tips of the anthers with its labellæ. Here *S. Dulcamara* seems to delude the fly as *Parnassia* and *Lopezia* do (590, III., pp. 20-22). *S. Dulcamara* is also visited by pollen-collecting *Bombi*, and pollen-feeding Syrphidæ (609).

314. *SOLANUM NIGRUM*, L.—The flowers are devoid of honey, but I have repeatedly seen two common Syrphidæ, *Melithreptus scriptus*, L., and *Syritta pipiens*, L., feeding on the pollen. Both stroked the outer side of the anthers with their labellæ from the apex downwards as far as the middle of the corolla. Sprengel observed bees and humble-bees upon the flowers. I have given a further account of the flower in No. 590, III.



FIG. 144.—*Lycium barbarum*, L.

1.—Flower, viewed from the front.  
2.—Ditto, in section.  
a, protecting hairs; st, stigma.

315. *LYCIUM BARBARUM*, L. (*L. vulgare*, Dun.).—Honey is secreted in large quantity by the naked ovary, and accumulates in the base of the tube, which is 7 to 10 mm. long. The corolla

widens out above, and is smooth within, except that a ring of close woolly hairs surrounds it at the base of the funnel-shaped, expanded portion; on a level with this ring, five similar rings of hairs surround the five stamens, and effectually exclude rain. The corolla divides above into five violet lobes, which spread out to a diameter of 16 to 22 mm. The funnel-shaped mouth is light-coloured, and marked with dark-violet lines (pathfinders) coursing towards the base of the flower. Stigma and anthers ripen together, and stand at the same height. The style is sometimes bent upwards above the anthers, as in the figure, but as a rule it is in immediate contact with them. Insect-visits, therefore, may lead equally well to cross- and self-fertilisation; and in absence of insects self-fertilisation in most cases takes place.

Visitors: Hymenoptera—*Apidæ*: (1) *Apis mellifica*, L. ♀, s., ab.; (2) *Bombus agrorum*, F. ♀, s.; (3) *B. lapidarius*, L. ♀, s., both very frequent. See also No. 590, III.

*Atropa Belladonna*, L., is likewise adapted for humble-bees. I have seen it visited by nine species of bees and by Thrips (590, III.).

*Mandragora vernalis*, Bert., is proterogynous, according to Hildebrand (351).

*Iochroma tubulosum*, Benth., is proterogynous with persistent stigmas. The deep-blue, pendulous flowers are tubular, widening out at the mouth, and are supposed by Delpino to be fertilised by humming-birds (177).

*Scopolia carniolica*, Jacq. (*S. atropoides*, Schult), is proterogynous (351).

316. *HYOSCYAMUS NIGER*, L.—Cross-fertilisation is insured, or at least favoured, by the prominent position of the stigma. Sprengel found the plant visited by humble-bees, and the dimensions of the flower seem well suited to these insects. I have seen only *Halictus cylindricus*, F. ♀, collecting pollen on the flower.

*Browallia elata*, L.—The corolla is hypocrateriform, and its mouth is blocked by the much expanded filaments of the two superior stamens, which are inserted in the throat of the corolla; these leave only two very narrow openings through which a thin proboscis may pass. The proboscis entering in this way touches the anthers (the inferior pair of which is inclosed in the tube), and also the stigma which stands between the two pairs of anthers; the stigma smears the entering proboscis with viscid matter in the

young flower, and receives pollen from it in the old. Delpino considers that the brown colour of the broad superior stamens is a device to guide insects that have alighted on the flower towards the pollen. His view that the flower is fertilised by Sphingidæ and Bombylidæ is opposed to this, for these insects seek honey only. Species of *Anthophora*, which Delpino thinks may possibly be also fertilisers, are likewise scarcely fitted to reach the pollen of *Browallia* (178, 360).

My brother Fritz Müller tells me, in a letter dated November 10, 1869, that he finds in the allied genus *Franziscea* (*Brunfelsia*)

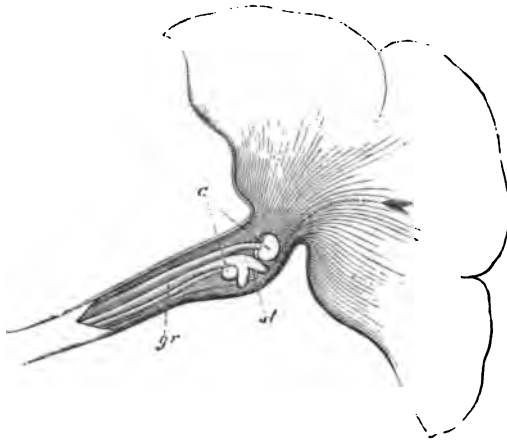


FIG. 145.

Flower of *Franziscea*, from Itajahy. Half of the corolla and two stamens have been removed.  
a, anthers; st, stigma; gr, style.

The dotted line indicates the path which the insect's proboscis must take to reach the honey.

a structure similar to that described by Delpino for *Browallia*. A handsome species of *Franziscea*, occurs at Itajahy. In this there are two lateral entrances to the tube, but between them the throat of the corolla is blocked, not by a valve formed by the stamens (*valvola staminale*, Delpino), but by the style which bends forward to apply itself to the anterior wall of the corolla.

*Schizanthus*, Rz. and P.—The two stamens are inclosed by the lower lip, and spring up when an insect settles on the latter: the stigma is at first shorter than the stamens, but after they have burst free it lengthens and projects beyond them, so as to be now the first part touched by an insect-visitor (346).

## ORD. SCROPHULARINEÆ.

317. *Verbascum nigrum*, L.—The long yellow racemes are very striking, and the flowers are made still more conspicuous by the orange-red anthers and violet hairs upon the filaments. The plant is visited by very various species of insects.

I sought repeatedly for honey without success, and had come to the conclusion that the flower contained none. On July 28, 1871, however, towards evening, I saw a small moth, *Ephestia elutella*, Hübner,<sup>1</sup> busy sucking very assiduously on the flowers of a plant of this species in my room. Standing on a petal, it thrust its proboscis down between two stamens<sup>2</sup> into the short tube, and applied it to various parts of the inner wall of the corolla. After spending a considerable time on one flower, it rolled up its proboscis and flew off to another. It continued these operations for some minutes, and therefore certainly found honey; and the next morning I found in many flowers, but not in all, minute drops of honey adhering to the smooth inner surface of the tube. The flowers afford a large quantity of orange-red pollen, accessible to all insects; and I observed that in the case of *Syrphus balteatus* the violet clavate hairs form a third attraction.

The position of the parts of the flower makes cross-fertilisation in case of insect-visits not inevitable but exceedingly likely, while in absence of insects self-fertilisation easily occurs. The short tube widens out into a flat, five-lobed limb, which takes up an almost vertical position: the inferior lobe is the longest, and the two superior are shorter than the lateral lobes, so that an insect settles most conveniently upon the inferior. The stamens project almost horizontally, but curve slightly upwards from the tube, and diverge slightly from one another; they alternate with the petals, and again the superior is the shortest and the two inferior longer than the lateral. The anthers, which stand close together, dehisce along their outer edge, covering themselves almost completely with orange-red pollen. The style is shorter than the inferior stamens, and bent down slightly below them. An insect standing on the inferior petal generally touches the knobbed stigma first, on its way

<sup>1</sup> Named for me by my friend Dr. Speyer, of Rhoden.

<sup>2</sup> Just between each pair of stamens, the central part of the corolla bears a chestnut-brown spot. Sprengel (702, p. 122) considered these spots to be honey-guides, though he could find no honey in the flowers. My discovery of honey confirms his view.

to the anthers; and thus cross-fertilisation is favoured, though stigma and anthers ripen together. In absence of insects, self-fertilisation is possible, as the stigma frequently stands in the line of fall of the pollen.

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus agrorum*, F. ♂, s.; (2) *B. terrestris*, L. ♀, s. and c.p.; (3) *Andrena pilipes*, F. ♀, c.p.; (4) *Prosopis signata*, Pz. ♀, f.p.; (5) *P. communis*, Nyl. ♀, f.p. B. Diptera—(a) *Bombylidae*: (6) *Systoechus sulfureus*, Mik., s.; (b) *Syrphidae*: (7) *Syrphus balteatus*, Deg., f.p. and licking the staminal hairs: (8) *Eristalis arbustorum*, L., do.; (9) *Syritta pipiens*, L., do. C. Lepidoptera—*Microlepidoptera*: (10) *Ephestia elutella*, Hübn., s. D. Coleoptera—*Nitidulidae*: (11) *Meligethes*, ab. E. Thysanoptera; (12) Thrips, ab. F. Neuroptera; (13) *Panorpa communis*, L., licking various parts of the flower.

318. *VERBASCUM PHENICEUM*, L.—The structure of the flower agrees with that of the preceding species, but I have hitherto failed, as Sprengel also did, to discover any honey; I have never seen any insect sucking on this flower. I once saw *Andrena fulva*, Schrank, ♀, insert its proboscis into three or four flowers and then immediately withdraw it; it then flew away, having doubtless failed to find anything.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, c.p.; (2) *Bombus muscorum*, L. ♀, c.p.; (3) *Andrena dorsata*, K. ♀, c.p.; (4) *A. fulva*, Schrank, ♀, vainly seeking honey; (5) *Halictus sexnotatus*, K. ♀, c.p.—I could see clearly how this bee loosened the pollen with its mandibles, and swept it with the tarsal brushes on its fore and midlegs into the collecting hairs on its hindlegs. B. Diptera—*Syrphidae*: (6) *Rhingia rostrata*, L., very ab., f.p.—I have often seen a specimen of this fly on almost every flower, eating pollen, and also licking the staminal hairs.

### 319. *VERBASCUM THAPSUS*, L. :—

Visitors: A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♂; (2) *Bombus Scrimshirani*, K. ♀; (3) *B. hortorum*, L. ♂; (4) *Halictus smeathmanellus*, K. ♀, all c.p.; (5) *H. cylindricus*, F. ♂; (6) *Andrena parvula*, K. ♂, both of these seemed to be sucking; (b) *Sphegidae*: (7) *Polistes gallica*, F. ♀ (Thur.), seemed also to be sucking. B. Diptera—*Syrphidae*: (8) *Helophilus florens*, L.; (9) *Syritta pipiens*, L.; (10) *Ascia podagrica*, F., all three f.p.

*Verbascum Lychnitis*, L.—I saw this species in Thuringia, visited by species of *Halictus* collecting pollen, and by Diptera and Coleoptera (590, III.).

Darwin, in *Forms of Flowers*, shows that *V. Thapsus* and *V. Lychnitis* readily produce hybrids in a state of nature; and that, since these hybrids are absolutely barren and the self-fertilised

plants fairly fertile, in this case insects-visits by promoting hybridisation do harm.

According to Delpino, the *Verbascums* are adapted for pollen-collecting bees, which, clinging to the hairs on the stamens, clear the pollen off the anthers and fly rapidly to another flower. I agree with this view, and look upon it as the most plausible explanation of the hairy stamens. But from my own observations it is clear that the small pollen-feeding bees (*Proscopia*) and *Syrphidæ* are very frequently the fertilisers of this genus. Delpino goes too far in saying that the flowers of *Verbascum* are adapted solely for bees (*esclusivamente melittophil*), and that the visits of all other insects are accidental and without significance (178, II., pp. 296-298).

*Calceolaria pinnata*, L.—Each of the two anthers is modified, as in *Salvia pratensis*, into a lever, of which one arm bears a pollenless anther-lobe and stands in the mouth of the corolla. When this arm is touched by an insect, it causes the other, the pollen-bearing lobe, to shed its pollen. Self-fertilisation may take place in the falling off of the corolla (352).

320. *LINARIA VULGARIS*, Mill.—The flowers which I have examined do not agree in all points with Sprengel's description. Honey is secreted by the base of the ovary, which is especially prominent anteriorly, opposite the lower lip. As a rule the honey does not, as Sprengel thought, leave the tip of the spur empty, flowing down at intervals in large drops which cannot reach the bottom for the air contained there; but it glides in a smooth, narrow groove, bordered by short, stiff hairs, which passes from the nectary between the two anterior stamens, and thence to the tip of the spur, which it fills to a depth of 5 or 6 mm. or even more. In several hundred flowers which I examined, I found two which corresponded in this point with Sprengel's description, so it seems probable that he based his account upon an abnormal specimen.

The adjacent sides of the two inferior stamens are closely beset with pointed processes at their base, which protect the honey from short-lipped insects, when such succeed, as ants frequently do, in entering the flower. The hairs bordering the groove protect the honey in like manner from insects, and also help to keep it in its course; the length of the spur would be of no advantage unless the honey were strictly confined to it.

The length of the spur (10 to 13 mm.) excludes short-lipped bees from the honey, and flies and beetles are prevented from entering the flower by the tumid lower lip, which completely

closes the tube; by these characters the flower becomes exclusively adapted for those most diligent of fertilising-agents, the long-probosced bees. The palate of the lower lip is of a bright orange colour, forming a "pathfinder"; guided by this, the bee presses down the lower lip, and creeps so far into the tube as to be able to thrust its head into the wide part of the spur and then reach the honey. In doing this, the back of the bee comes in contact with the anthers and stigma; these are matured simultaneously, and the stigma lies between the shorter and longer pairs of stamens, so that the bee can bring about both cross- and self-fertilisation. Probably, if pollen from another and from the same flower are applied to the stigma, the former outstrips the latter. In absence of insects, self-fertilisation is possible. The visitors consist exclusively of bees.

Visitors: Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♂, very ab. To suck, it creeps almost entirely into the flower and thrusts its head into the wide entrance of the spur, which it empties down to a depth of 2—3 mm. It creeps out again with its back covered with pollen, and proceeds more frequently to flowers at the same height on neighbouring plants than to higher flowers on the same. In other cases I have seen the honey-bee bite a hole in the spur, and empty it, as Sprengel describes. Sprengel has correctly described its behaviour while collecting pollen: "It slightly separates the lower lip of the corolla from the upper, and thrusts its head so far in as to reach the anthers and obtain their pollen." (2) *Bombus terrestris*, L. ♀, sucking normally. It inserts its head, thorax, and forelegs, into the flower, then thrusts its proboscis (7—9 mm.) almost to the tip of the spur, and emerges with the upper surface of its head, pro- and meso-thorax thickly covered with pollen. Sometimes it sweeps off part of this pollen with the brushes on its fore and midlegs, and places it on the hindlegs. Sprengel's idea that the large humble-bees do not enter the mouth of the flower is accordingly erroneous. (3) *Bombus hortorum*, L. ♀ ♀ and ♂. I have very frequently seen this bee empty the flowers of their honey, which it can do more quickly owing to the length of its proboscis (17—21 mm.) than the preceding species. Even the males sometimes swept the pollen off their heads with their forelegs, and always had a number of pollen-grains on all their tarsal brushes; (4) *Megachile maritima*, K. ♂ (8—9), s.; (5) *Osmia ænea*, L. ♀ (9—10), repeatedly, s. and c.p.; (6) *O. leucomelæna*, K. (parvula, Duf.), ♀ (2½), c.p.; (7) *Anthidium manicatum*, L. ♀ ♂ (9—10), ab., both s. and (♀) c.p.; (8) *Andrena Gwynana*, L. ♀ (2½), c.p.; (b) *Formicidæ*: (9) Various species, ab., s.

Delpino observed *Linaria vulgaris* fertilised by the hive-bee and by *Bombus italicus* (172).

*Linaria alpina*, Mill., is likewise adapted for humble-bees, but is visited by Lepidoptera also (609).

*Linaria minor*, Desf., is very rarely visited by insects, and fertilises itself regularly (590, III).

*Linaria Cymbalaria*, Mill. is visited chiefly by bees (590, III.). Cleistogamic flowers occur in *Linaria* according to Michalet (524) and Kuhn (399).

321. *ANTIRRHINUM MAJUS*, L.—This plant differs from *Linaria vulgaris* (1) in the much greater size of its flowers, into which our largest humble-bees can enter bodily, (2) by its more firmly closed entrance, which excludes the smaller bees, (3) in its nectaries and honey receptacles.

The honey is secreted, as Sprengel suggested, by the smooth, green, fleshy base of the ovary, whose upper part is paler in colour and covered with fine hairs; but it does not flow, as Sprengel thought, down into the short spur—which is hairy within, and for that reason unfitted to be a honey-receptacle, but it remains adherent to the nectary and to the base of the anterior stamens. The short wide spur permits the insect's proboscis to reach the honey from below; above and in front it is protected by a thick fringe of stiff, knobbed hairs on the angles of the anterior stamens.

The flowers are fertilised chiefly by humble-bees, of which I have observed the following species: (1) *Bombus hortorum*, L.; (2) *B. terrestris*, L.; (3) *B. agrorum*, F.; (4) *B. silvarum*, L.; (5) *B. lapidarius*, L. The females and workers, and in late summer the males also, creep bodily into the flower, and creep out backwards dusted on their backs with pollen. From time to time they brush off the adhering pollen from their thorax with the tarsal brushes of the fore and midlegs, and from the abdomen with the tarsal brushes of the hindlegs. Not only the females and workers, but the males also, perform this action, which seems, therefore, to be done more for cleanliness than to collect the pollen, though the females and workers naturally make use of it, placing it in the pollen-baskets on their hindlegs. I have also seen *Anthidium manicatum*, L. ♀, *Megachile fasciata*, Sm. ♂, and *Osmia rufa*, L. ♀, creep into the flower and emerge with their backs covered over with pollen. Smaller bees only exceptionally creep into still fresh flowers, and are useless to the plant: I have only once seen *Megachile centuncularis*, L. ♀, succeed in entering; on the other hand I have repeatedly seen small species of *Halictus* (*H. zonulus*, Sm. ♀, *H. morio*, F. ♀, *H. Smeathmanellus*, K. ♀) flying from flower to flower until they reached an old flower, which in withering had opened slightly and permitted them to enter. This showed clearly how far the fast closure of the mouth is useful to the plant; if the small bees could enter from the first, they would use up much of the honey,

and the flowers would be less diligently visited by the humble-bees.

Dr. Ogle found that *Antirrhinum* produced no seed when protected from insects by a tent of gauze (632).

*Maurandia*, Ort., *Chelone*, L., and *Pentstemon*, L'Her., are, according to Delpino, proterandrous, the style coming to occupy the place of the stamens. In the two last genera, the stamens are broad, fleshy, and hollowed out at the base to secrete and lodge the honey. *Pentstemon* is fertilised by *Bombus*, *Anthidium*, and *Apis*. (178, 360). The position of the fifth stamen in *Pentstemon* and its frequent partial or complete abortion has been discussed by Dr. Ogle (632). A very thorough account of the floral mechanism of *Pentstemon* is given by Errera (230).

322. *SCROPHULARIA NODOSA*, L.—In most Lamiales and Personales the anthers lie in two pairs, one behind the other, and

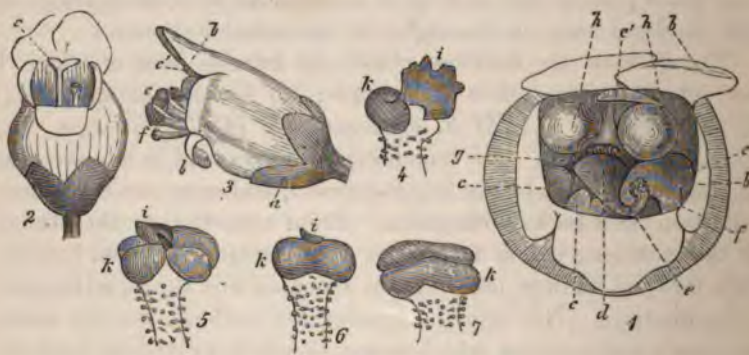


FIG. 146.—*Scrophularia nodosa*, L.

- 1.—Flower, in first stage, from the front ( $\times 7$ ).
- 2.—Ditto, from below ( $\times 3\frac{1}{2}$ ).
- 3.—Older flower, fertilising itself, viewed from the side.
- a, calyx; b, corolla; c, stamen; c', fifth metamorphosed stamen; d, ovary; e, style; f, stigma; g, nectary; h, drop of honey.
- 4-7.—Fifth stamen in various stages of reversion towards its original form ( $\times 12$ ).  
i, black membranous lobe; k, anther-lobe.

touch an insect-visitor on the dorsal surface; the stigma then, to insure cross-fertilisation, must also touch the insect on the back, and the style can scarcely lie elsewhere than between the two pairs of stamens, along the upper part of the corolla. The superior stamen comes in the way, and accordingly disappears;<sup>1</sup> it has no chance of reappearing permanently, for it is directly injurious, and is weeded out by natural selection. I have only once found a flower of

Cf. Dr. Ogle, No. 632, p. 51.

*Lamium album* with five stamens; the upper lip was absent, and the fifth stamen, which stood behind the other four, was well formed, but shorter than the others.

In *Scrophularia*, on the other hand, the anthers come in contact with the ventral surface of the insect. The fifth stamen is thus useless, but not injurious; whether it be present or absent is of no importance, and it is therefore beyond the influence of natural selection. Accordingly, the small black scale-like appendage on the upper wall of the corolla in *Scrophularia* (c, 1, 2, 3), which represents the fifth stamen, shows not unfrequently more or less complete reversion to its primitive form (4-7, Fig. 146). The more completely it approaches its typical form, the more perfect also are the pollen-grains which it bears; thus in the anther *k*, 4, not half of the pollen-grains attained the normal size ( $\frac{5}{32}$  mm. in diameter); most of them were much smaller ( $\frac{2}{32}$  mm.) and shrunk; in the anther *k*, 7, only a few pollen-grains fell short of the normal size. In exceptional cases the anther even dehisces, and lets part of its pollen escape.

The flowers of *Scrophularia* are remarkable for being specially visited by wasps. The wide globular corolla is about 5 mm. in diameter, and in its base, near the superior side, two large drops of honey may be seen, which are secreted by the yellowish base of the ovary. Wasps visit the flowers in great numbers; clinging with all six legs to the outside of the flower, with the abdomen applied to it below, they easily insert their heads between the upper and lateral lobes of the corolla and reach the honey with very little loss of time.<sup>1</sup> In young flowers they touch the stigma, and in old flowers the anthers with the under-side of the head and of the pro- and meso-thorax, and thus regularly fertilise younger flowers with the pollen of old, as Sprengel showed. Severin Axell's doubts regarding the possibility of proterogynous dichogamy in entomophilous flowers may be easily refuted by observing *Scrophularia* in flower in the open air. For, as Sprengel showed and as I have repeatedly observed, flowers are constantly to be seen whose stigmas are covered with pollen, but whose anthers are still unripe and hidden within the corolla. Sprengel is wrong in saying that fertilisation can only be effected by insects. The stigma, when supplied with pollen by insects, bends down over the lower lip and withers, while the anthers ripen and project beyond the lower border of the corolla; but in absence of insects, as I have frequently seen in plants flowering in my

<sup>1</sup> See Sprengel (702), Title-page, fig. xxv.

room, the stigma remains fresh and outstretched, while the anthers dehisce immediately above, letting part of their pollen fall upon it. I have likewise observed on plants in my room that such self-fertilisation regularly produces capsules filled with well-formed seeds. In long-continued cold and wet weather, when neither wasps nor bees are about, all the capsules of *Scrophularia* are well filled.

In sunny weather cross-fertilisation never fails, for all our wasps, except *V. Crabro*, are frequent visitors.

According to Mr. A. S. Wilson, wasps on *Scrophularia* begin at the top of the inflorescence and proceed downwards; so that here the crossing of *separate plants* is insured just as it is in proterandrous plants with elongated inflorescences (*e.g.* Labiatae), where the fertilising-agents (bees) proceed from below upwards (778).

Hymenoptera—(a) *Vespidæ*: (1) *Vespa vulgaris*, L.; (2) *V. rufa*, L.; (3) *V. germanica*, F.; (4) *V. media*, Deg.; (5) *V. holsatica*, F., all s., very ab.; (b) *Apidæ*: (6) *Bombus agrorum*, F. ♀ ♀, s., scarce; (7) *Halictus sexnotatus*, K. ♀, s. and c.p.; (8) *H. zonulus*, Sm. ♂, s.; (9) *H. flavipes*, F. ♂, s. See also No. 590, III.

*Scrophularia aquatica*, L.—The floral mechanism and the insect-visitors are similar to those of *S. nodosa* (590, III.).

*Scrophularia* occurs with cleistogamic flowers (Kuhn, No. 399). The most thorough account of the fertilisation of *Scrophularia* is given by Mr. W. Trelease, who also gives a *résumé* of the special literature (737).

*Collinsia bicolor*, Bth., and *C. verna*, Nutt.—In these flowers the stamens and style lie near the lower side of the flower; the fifth stamen, modified into a honey-gland, and the honey-receptacle, which consists of a pouch near the base of the corolla, are on the upper wall. The flower imitates very closely the Papilionaceous type, even to the production of alæ, vexillum, and carina. (Delpino, No. 178). In absence of insects, the flowers fertilise themselves, and are fertile to their own pollen (360).

*Mimulus luteus*, L. (*M. guttatus*, D.C.)—Bees entering the flower touch first the inferior lobes of the stigma, which cover up the anthers. Immediately afterwards the stigmatic lobes fold up and expose the anthers to be touched by the bee, which thus becomes dusted with fresh pollen (Batalin, No. 38).

The case of *M. Tillingii* is quite similar (Behrens, No. 49).

*Glossostigma elatinoides*, according to Cheeseman, has a similarly irritable stigma (132).

*Mimulus (Diplacus) glutinosus*, Wendl., var.  $\beta$  (*D. puniceus*, Nutt.), behaves in the same manner (Hildebrand, No. 352).

*Vandellia*, L., has cleistogamic flowers (399).

323. *DIGITALIS PURPUREA*, L.—Honey is secreted by an annular ridge surrounding the base of the ovary (*a*, 1, 2, Fig. 147). This ridge is not 'covered thickly with short hairs' as Sprengel described it, but is perfectly smooth; the ovary only becomes hairy *above* the ridge.

The anthers and stigma lie pointing downwards near the upper wall of the corolla. The longer stamens are ripe before the shorter ones, and these before the stigma. The dimensions of the flower

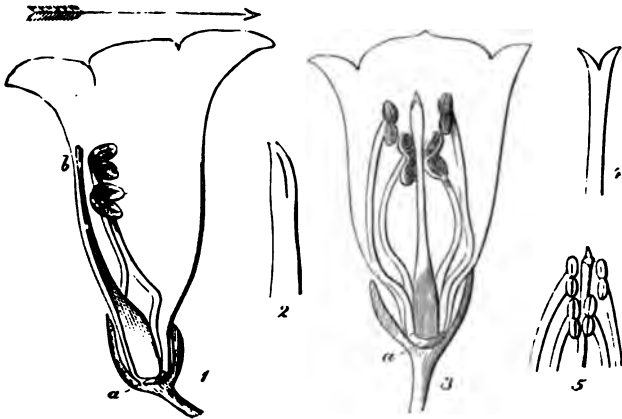


FIG. 147.—*Digitalis purpurea*, L.

1.—Young flower after removal of the right half of the calyx and corolla. The taller anthers are on the point of dehiscing. This figure should be turned round horizontally in the direction of the arrow.

2.—Tip of style of the same flower, enlarged.

3.—A somewhat older flower. The taller anthers are now empty, the shorter pair are dehiscing and are covered with pollen. Viewed from below, after removal of the lower half of the calyx and corolla.

4.—Tip of style of the same flower.

5.—Empty anthers and stigma of an old flower, from below.

suggest that it is adapted for humble-bees, for no other native insects are large enough to touch the stigma and anthers with their backs when creeping into the tube; and, as a matter of fact, humble-bees are the only fertilisers of the Foxglove. Sprengel, on the title-page of his work, represents *B. terrestris*, ♀, creeping into this flower. When bees frequent the plant abundantly, all the four anthers are emptied of their pollen before the stigmatic lobes (*b*, 1, Fig. 147) separate. In absence of humble-bees, the anthers remain covered with pollen until the stigmatic lobes have spread apart; and then when the corolla falls off this pollen is

brought in contact with the stigma, or some may even have fallen on the stigma previously. The flowers almost always bear seed, even in long-continued rainy weather, and therefore it is probable that self-fertilisation is effective; Hildebrand's experiments are no evidence of the contrary, for he only showed that the stigma before opening is incapable of fertilisation (342). The large, widely-open flowers, naturally receive many unbidden and useless guests. If the plant is thus at a disadvantage in comparison with *Antirrhinum*, it has at least the advantage of letting its fertilising agents do their work more quickly, visiting more flowers in a given time.

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus terrestris*, L. ♀; (2) *B. hortorum*, L. ♀; (3) *B. agrorum*, F. ♀, all three ab., s.; (4) *Andrena coitana*, K. ♀ (Sld.), ab., c.p.; (5) *Halictus cylindricus*, F. ♀, ab., c.p. B. Coleoptera—(a) *Nitidulidæ*: (6) *Meligethes*, very ab.; (b) *Cryptophagidæ*: (7) *Antherophagus pallens*, Ol., scarce; (c) *Malacodermata*: (8) *Dasytes*. The last five are quite useless visitors.

*Digitalis lutea*, L., is fertilised by *Bombus hortorum*, L., which can only insert its head into the corolla (609).

*Digitalis ambigua*, Murr. (*D. grandiflora*, Lam.), is fertilised by humble-bees, which creep bodily into the corolla. The flower is protogynous, and bees begin at the base of the raceme and proceed upwards (590, III.; 609).

324. VERONICA CHAMÆDRYS, L.—Honey is secreted by a yellowish fleshy disk below the ovary, and lies in the base of the tube sheltered from rain by hairs on the corolla. The flowers are rendered conspicuous by their bright blue colour, and by association in racemes; dark blue radiating lines and a central white spot on the limb of the corolla guide insects towards the honey. The anthers and stigma ripen together; the style points obliquely downwards in front of the anterior (inferior) petal, the two stamens diverge on either side, and stand opposite to the lateral petals; fertilisation can therefore only be effected by the aid of insects. The anterior petal forms the most convenient landing-place, and the stigma is usually touched before the anthers by the ventral surface of the insect. The insect next tries to cling to the entrance of the short tube with its forelegs, and in doing so it catches hold of the thin, flexible bases of the stamens: quite unintentionally it draws the stamens inwards beneath it, and dusts its ventral surface with pollen. The thinning of the style at its base is another adaptation towards this plan of cross-fertilisation, for it insures that the stigma shall be touched by the ventral

surface of the insect, and allows of the style being so slightly inclined that its presence does not interfere with the insect when alighting. An insect alighting on one of the lateral petals sometimes draws the stamen opposite to this petal against its body, but with far less certainty. The chief visitors are *Syrphidæ*.

Visitors: A. Diptera—*Syrphidæ*: (1) *Rhingia rostrata*, L., s., freq.; (2) *Melanostoma mellina*, L.; (3) *Ascia podagrica*, F., both very abundant. I repeatedly saw both effecting cross-fertilisation in the manner described. B. Hymenoptera—*Apidæ*: (4) *Apis mellifica*, L. ♀, c.p.; (5) *Andrena Gwynana*, K. ♀; (6) *A. fulvicrus*, K. ♀; (7) *Halictus longulus*, Sm. ♀, the last three both s. and c.p. C. Coleoptera—*Cistelidæ*: (8) *Cistela rufipes*, F., devouring the anthers. See also No. 590, III., and No. 609.

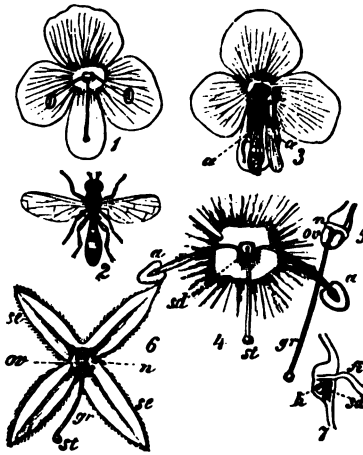


FIG. 148.—*Veronica Chamædrys*, L.

- 1.—Flower, viewed from the front.
  - 2.—Small fly (*Ascia podagrica*, *Syrphidæ*) hovering in front of the flower, attracted by its colour.
  - 3.—Flower at the moment when the fly, alighting on the inferior petal, grasps the bases of the filaments, and strikes the anthers together against the under surface of its body.
  - 4.—Centre of the flower, twice as much enlarged.
  - 5.—Pistil and nectary.
  - 6.—Calyx, with pistil and nectary.
  - 7.—Tube in longitudinal section.
- ad*, protecting hairs; *gr*, style.

*Veronica urticifolia*, L., has a similar floral mechanism to that of *V. Chamædrys*, and is likewise fertilised by *Syrphidæ*. The honey is quite exposed without any contrivance to shelter it. The flowers are rose-pink, which is probably a more primitive colour than blue both in *Veronica* and in *Myosotis* (589, 609).

*Veronica montana*, L., is more conspicuous and more abundantly visited by insects than *V. Chamædrys* (590, 609).

325. *VERONICA BECCABUNGA*, L.—This species agrees with *V. Chamædrys* in regard to its nectaries and also in the means adopted

for sheltering and pointing out the honey. It differs from it only in certain apparently trivial points, viz. in the development and position of the style and stamens:—yet these apparently trifling differences greatly influence the mode of fertilisation and the possibility of self-fertilisation in the absence of insects.

When the flower opens, the stigma is already well-developed; it is provided with long papillæ, and capable of holding fast pollen applied to it. The anthers still remain closed. The stamens and style project forwards in a straight line from the flower and afford a standing-place for insects. In cold, windy, or rainy weather the flowers only open partially, and the anthers remain in contact with the stigma, leading to regular self-fertilisation. In warm sunshine the petals expand widely, coming to lie almost in one plane; the stamens are caused thereby to diverge more and more, and the anthers are thus removed to a distance from the stigma before



FIG. 149.—*Veronica Beccabunga*, L.

- 1.—Flower, viewed obliquely from above, so that the upper petal is foreshortened ( $\times 3$ ).
  - 2.—Corolla, after removal of the stamens, viewed from the front ( $\times 3$ ).
  - 3.—Flower, after removal of corolla and stamens, seen from the side ( $\times 7$ ).
- a, calyx; b, corolla; c, stamen; d, ovary; e, style; f, stigma; g, nectary (green); h, protecting hairs.

dehiscing. Insects frequent the plant in considerable numbers. The most abundant visitor is a small species of Syrphidæ, *Syrifta pipiens*, L.; hovering backwards and forwards in its jerky flight before the flowers, it suddenly alights on one; sometimes it settles on the projecting style and stamens, which bend beneath its weight, and creeps forward a step or two in order to thrust its proboscis (3 mm. long) into the tube (1 mm.); sometimes it alights on the anterior or on one of the lateral petals, and pulls down one of the stamens with its forefeet until it can reach the pollen with its proboscis. It thus brings various parts of its body in contact with the anthers and stigma, and performs sometimes cross-fertilisation, sometimes self-fertilisation. Most usually cross-fertilisation results, for the insect alighting on the projecting style and stamens usually touches the stigma with the ventral surface of its body, already dusted with pollen. A smaller species of Syrphidæ, *Ascia podagrica*, F., visits

the flowers very abundantly and in a similar way. All other visitors come as stragglers.

A. Diptera—(a) *Syrphidæ*: (1) *Syritta pipiens*, L.; (2) *Ascia podagrica*, F.; (3) *Eristalis sepulcralis*, L., s. and f.p.; (b) *Muscidæ*: (4) *Scatophaga stercoraria*, L., s. and f.p., also several small *Muscidæ*. B. Hymenoptera—*Apidæ*: (5) *Apis mellifica*, L. ♀, s.; (6) *Andrena parvula*, K. ♀, s. and c.p.; (7) *Halictus sexstrigatus*, Schenck, ♀, s. and c.p.

326. *VERONICA OFFICINALIS*, L.—The flowers do not open so widely even in warm sunshine as do those of *V. Chamædrys*. In fully expanded flowers the upper and lower petals only diverge at an angle of 70° to 80°, and the two lateral petals at 90° to 100°. The two stamens, which are very thin at the base, project from the flower at an angle of 30° to 40° from one another, and from the style which stands below them. Insect-visitors touch the stamens and stigma with various parts of their bodies, and lead to cross- and self-fertilisation indiscriminately. In flowers kept in the house and protected from insects, the stamens bend inwards and downwards as they begin to wither until they touch each other and the stigma, producing self-fertilisation. The thinning at the base of the stamens, which in *V. Chamædrys* was shown to assist insects to perform cross-fertilisation, is here seen to aid self-fertilisation only.

A. Diptera—(a) *Empidæ*: (1) *Empis livida*, L., s., ab.; (b) *Syrphidæ*: (2) *Helophilus floreus*, L., s.; (3) *Syritta pipiens*, L., ab., s. B. Hymenoptera—*Apidæ*: (4) *Halictus albipes*, F., c.p.; (5) *Bombus* (*Apathus*) *vestalis*, Fourc. ♀, s.; (6) *B. Barbutellus*, K. ♀, s.,—this large bee seemed dissatisfied with the small amount of honey, for after visiting a few flowers it went off to *Glechoma hederacea*. See also No. 609.

327. *VERONICA SPICATA*, L. (Thuringia).—*V. spicata* shows a remarkable tendency to vary between proterandrous and protogynous dichogamy. On many plants, the style protrudes before the flower is fully opened (b, 4), and curves downwards and ripens its stigma before the anthers dehisce (b, 5). On other plants, when the flower opens, the style is much shorter than the stamens (b, 1, 2), and only reaches its full length and ripens its stigma when the anthers have been emptied of their pollen (b, 3).

On plants of both sorts, flowers not unfrequently occur whose styles never reach their full development, but remain concealed in the tube; and on some plants this is the case throughout all the flowers. These aborted styles are often double (b, 8). Honey is secreted by the fleshy base of the ovary (h, 6, 7); it lies in the

tube of the corolla, which is about 2 to 3 mm. long, and is sheltered from rain by a ring of long stiff hairs at the mouth of the tube. In case of insect-visits, cross-fertilisation is insured by the proterandrous or proterogynous condition, and by the situation of the stigma which projects beyond the anthers. I have never observed



FIG. 150.—*Veronica spicata*, L.

- 1.—Flower, shortly before dehiscence of the anthers (a), viewed from the front. The stigma (b) is still immature, and stands far below the anthers.  
o, superior petal; ss, lateral, u, inferior, petals.
- 2.—Ditto, somewhat more expanded, from the side.
- 3.—Ditto, from the side. The anthers have withered; the stigma is mature, and stands below and in front of the anthers ( $\times 3\frac{1}{2}$ ).
- 4.—Young flower, from another individual. The style already protrudes from the flower, and the stigma is so far developed that pollen readily adheres to it. The anthers are still closed and concealed within the tube.
- 5.—Another somewhat older flower, from the same individual, viewed from the front. The stigma is fully ripe, the anthers are in the act of dehiscing ( $\times 3\frac{1}{2}$ ).
- 6.—Ovary and nectary (h) from the side.
- 7.—Nectary, after removal of the ovary, from above.
- 8.—An ovary, with two imperfect styles ( $\times 7$ ).

self-fertilisation, though it may now and then take place by pollen falling on the stigma.

Visitors: Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, c.p., or s.; it even thrusts its proboscis into the lowest, oldest flowers whose corollæ have fallen off; (2) *Prosopis communis*, Nyl. ♀ ♂, s.; (b) *Sphegidae*: (3) *Psammophila viatica*, L. ♂, s.; (4) *Cerceris labiata*, F. ♀ ♂, ab., s.; (5) *C. nasuta*, Kl. s.

Near Bozen according to Gerstäcker, *V. spicata* is visited chiefly by species of *Xylocopa* (*X. violacea*, L., *X. cyanescens*, Brullé, *X. valga*, Gerst.).

328. *VERONICA HEDERÆFOLIA*, L.—The small, solitary, pale flowers are less conspicuous than those of any other species described here; they are very seldom visited by insects, but almost without exception bear good seed, and the species is one of the commonest of

its genus. The presumption that this results from self-fertilisation is increased by watching the plant when protected from insects. When the flower opens, the anthers are seen to have already dehiscent, and to have their pollen-covered surfaces applied to the stigma. I have myself observed that when insects are excluded the plant regularly bears good seed.

The honey is secreted and sheltered as in *V. Chamædrys*; the stamens are however not thinned at their bases. Even in case of insect-visits, cross-fertilisation is not rendered more probable than self-fertilisation; but when it does occur, its action probably has the mastery.

I have only seen this flower visited by insects occasionally in the first sunny days of spring; later in the season, the competition of other flowers causes it to be neglected.

Visitors: Hymenoptera—*Apidae*: (1) *Andrena parvula*, K. ♀, s.; (2) *Halictus nitidiusculus*, K. ♀; (3) *H. leucopus*, K. ♀; (4) *H. albipes*, F. ♀, all three rather abundant, sucking on a small slope where few other plants were in flower (April 11, 1869).

*Veronica agrestis*, L., possesses the same floral mechanism as *V. Chamædrys*, but in an imperfect or rather in a retrograde condition (590, III.).

329. *VERONICA SERPYLLIFOLIA*, L.—The flowers are rendered more conspicuous than those of *V. hederæfolia*, by dark violet lines



FIG. 151.—*Veronica serpyllifolia*, L.

1.—Flower, front view.  
2.—Diagram of ditto  
a, stigma; b, stamen; c, petal; d, sepal.

on the superior and lateral petals. They are doubtless more visited by insects, and more frequently cross-fertilised; and accordingly self-fertilisation does not take place at so early a stage.

In many flowers, the anthers are at first closed, while the stigma is fully ripe; in this condition, insect-visits naturally lead at once to cross-fertilisation. In most flowers, on the other hand, the stigma and anthers ripen together; the anthers stand more

or less close above and at the sides of the stigma, turning their pollen-covered faces towards it; in many cases they stand so close that the pollen in being forced out is directly applied to the stigma.

On plants which I kept in my room, I have seen *Calliphora erythrocephala*, Mgn. (Muscidæ), sucking honey and fertilising the flowers. It thrust its proboscis several times into each, and therefore where anthers and stigma had ripened together, it performed cross- and self-fertilisation indifferently.

*V. saxatilis*, Scp. (*V. fruticans*, Jacq.).—The small, but brightly coloured flowers of this plant are fairly conspicuous, and secrete abundant honey. The visitors are numerous, and the mechanism of fertilisation is the same as that of *V. Chamædryas*.

*V. bellidioides*, L., has no trace of the special adaptations for cross-fertilisation that *V. Chamædryas* shows. Insect-visitors are scarce, and cross-fertilisation can only take place if they happen to touch the stigma and anthers with different parts of their bodies.

*V. alpina*, L.—The tiny flowers are very rarely visited by insects, and in dull weather they remain closed and fertilise themselves.<sup>1</sup>

#### REVIEW OF THE GENUS VERONICA.

In this genus, as in *Polygonum*, *Geranium*, and others, the certainty of cross-fertilisation in case of insect-visits, and the abandonment of the power of self-fertilisation even in absence of insects, run parallel with the conspicuousness of the flowers and the consequent certainty of their being visited. The chief species that we have discussed may be arranged in the following order of conspicuousness, taking into account the appearance of the whole inflorescence:—(1) *V. spicata*, (2) *V. Chamædryas*, (3) *V. officinalis*, (4) *V. Beccabunga*, (5) *V. scutellarioides*, (6) *V. hederifolia*. In case of insect-visits, cross-fertilisation is rendered absolutely certain in the first, and extremely probable in the second of these, but in all the rest self-fertilisation is just as likely. In absence of insects, on the other hand, self-fertilisation never or very rarely takes place in the first and second; in the third it occurs regularly, but only when the flower withers; in the fourth, it regularly takes place in

<sup>1</sup> Lists of visitors to the following additional species of *Veronica* are given in my *Worms and Insects*, Pt. III:—*V. Lychnis*, L., *V. angustifolia*, L., *V. serpyllifolia*, L.; and the following are discussed and figured in my *Epiphytæ*:—*V. alpina*, L., *V. spicata*, L., *V. hederifolia*, L., *V. saxatilis*, Scp.

dull weather while the flower is still fresh; in the fifth it occurs in many flowers, and in the sixth in all, at the very outset. The honey is secreted and guarded in much the same manner in all six species, and so the likelihood of insect-visits can only depend upon the conspicuousness of the flowers.

*Wulfenia carinthiaca*, Jacq., is proterogynous (Hildebrand, No. 351).

*Bartsia alpina*, L., is proterogynous, and is fertilised by humble-bees. The stigma and anthers have the same relative positions as in *Rhinanthus major* (Fig. 156). Self-fertilisation is impossible (609).

330. ODONTITES SEROTINA, Rchb. (*O. rubra*, Pers., *Euphrasia Odontites*, L.).—Honey is secreted by the lower parts of the ovary, which is smooth, and swollen anteriorly (*b*, 6), while the upper part



FIG. 152.—*Odontites serotina*, Rchb.

- 1.—Bud, with exserted stigma ( $\times 3\frac{1}{2}$ ).
- 2.—Flower, with the stigma lying between the anthers.
- 3.—Flower, whose style projects far beyond the anthers.
- 4.—Flower, in which the style lies to one side.
- 5.—The two stamens of the left half of the flower, seen from the inside ( $\times 7$ ).
- 6.—Ovary.

*a*, base of the corolla; *b*, nectary; *c*, upper hairy part of the ovary; *d*, style; *e*, hairs which unite the anthers; *f*, hairs which prevent pollen from being scattered at the sides; *g*, sharp teeth which prevent the bee from thrusting its proboscis between the bases of the filaments; *h*, path taken by the bee's proboscis.

(The flowers 2 and 4 should slant more forwards than they are here figured.)

is hairy: it is lodged in the base of the corolla, whose tube is 4 to 5 mm. long, and smooth within; the broad stamens, which almost block the entrance of the tube, guard it from rain, and two to four purple spots at the base of the lower lip serve as guides towards it. The stamens almost touch each other below, where they are covered on their inner sides with sharp points; close under the anthers they are smooth and lie more widely apart. A bee, after alighting on the three-lobed under-lip, which affords a convenient landing-place, can only thrust its proboscis into the flower close

below the anthers, in the position *h*, 2, and in doing so it cannot fail to touch the downward-pointing ends of some of the anthers. The four anthers are held together posteriorly by matted hairs (*e*, 5), and anteriorly dehisce from the apex inwards (5, Fig. 152) by a wide fissure; so that a single touch on the part of the bee is communicated to all the anthers, and causes them all to shed a part of their dry, dusty pollen. Hairs directed downwards at the edges of the anthers (*f*, 5) prevent the pollen being scattered at the sides, so that great part falls on the bee's proboscis, and is carried to the stigma of another flower.

The development of the flower of *Odontites serotina* varies in a peculiar manner, and seems to depend upon the more or less sunny nature of the spot. The style bearing the fully-developed stigma usually projects far out of the bud shortly before it expands (1, Fig. 152), and the flower can therefore be cross-fertilised when it is scarcely open. In shady places, for instance among corn, the style lags behind while the corolla and stamens continue to grow, so that the stigma stands between the taller anthers and gets self-fertilised (2, Fig. 152). From the great productiveness of all the capsules in shady places where insect-visits are rare, we may conclude that such self-fertilisation is efficient. In sunny spots the style continues to grow along with the corolla and stamens, and overtops the anthers to the last; it may either lie above the latter (3, Fig. 152) or project at the side (4, Fig. 152). In this case, the stigma can only receive pollen by the aid of insects, and from other (either older or younger) flowers. Although this difference seems in general to depend upon the sunny or shady character of the spot, other unknown conditions (perhaps heredity) must co-operate; for I have sometimes observed in the same spot, and even on the same plant, flowers which fertilised themselves, and others incapable of doing so.

An imperfection in the flowers deserves special mention. The upper lip, as the figure shows, projects so slightly that the anthers in great part protrude beyond it and are unprotected. This is sometimes the case to such a degree that bees thrust their tongues into the flower above the stamens, and thus suck honey and shake out the pollen without leading to fertilisation.

I have only seen bees visiting this plant.

(1) *Apis mellifica*, L. ♀, very ab., thrusting its proboscis into the flower usually below the stamens, but sometimes above them,—it inserts its proboscis even into young unexpanded flowers, with long exerted styles; (2) *Bombus lapidarius*, L. ♀, s.; (3) *B. silvarum*, L. ♀, s.

331. *ODONTITES LUTEA*, Rchb. (Rehmberg, near Mühlberg, Thuringia).—Honey is secreted by the smooth lower half of the ovary, which is hairy above; it lies in the base of the corolla-tube, which is  $2\frac{1}{2}$  mm. long, and is smooth within, but provided with reflexed hairs at its mouth. The stamens stand apart, but from the small size of the flower they are all easily touched at the same time by an insect; there is no provision of hairs to prevent scattering of the pollen; the slits by which the anther-lobes dehisce are narrower than in *Euphrasia officinalis*. The style often protrudes from the bud (3, Fig. 153), and Hildebrand describes the flower as proterogynous; in other cases it is bent backwards in the bud, under the lower lip, and emerges together with the stamens on the opening of the flower. The stigma comes to maturity at the



FIG. 153.—*Odontites lutea*, Rchb.

- 1.—Flower, from the side ( $\times 3\frac{1}{2}$ ).
- 2.—Ditto, from the front.
- 3.—Bud, from the side.
- 4.—Anther.

same time as the anthers, and stands below and in front of them; it is, therefore, usually touched first by insect-visitors. In absence of insects, some pollen generally falls upon the stigma. I have only once (August 28, 1869) seen a bee, *Bombus muscorum*, L. ♂, sucking honey on the flower.

*Euphrasia minima*, Schleich., is sparingly visited by insects, and in their absence it fertilises itself regularly. The flower resembles in structure the small-flowered form of *E. officinalis* (i.e. *E. gracilis*, Jord.) (609).

332. *EUPHRASIA OFFICINALIS* (L.), Schk.—Honey is secreted and sheltered as in *Odontites scrotina*. The tube of the  
4 to 6 mm. long, but widens considerably at the outer e

an insect with a proboscis less than 4 mm. long can reach the honey by thrusting its head into the wide part of the tube.

The upper lip forms a vaulted roof over the stamens; it shelters the honey at the base of the tube from rain, and prevents an insect's proboscis from being thrust in above the stamens, as was possible in *Odontites serotina*. The three-lobed under-lip forms a convenient landing-place for the smaller visitors, and affords foothold for the forelegs of larger ones. An orange spot on the under lip, another at the entrance of the tube, and dark violet lines converging towards the mouth on both upper and lower lips, serve as



FIG. 154.—*Euphrasia officinalis*, L.

- 1.—Flower of the small-flowered form, seen from the front ( $\times 7$ ).
  - 2.—The two stamens of the right half of the flower, from the outer side.
  - 3.—Ditto, more magnified, from the inner side.
  - 4.—Flower of the large-flowered form, just after opening, from the side ( $\times 3\frac{1}{2}$ ).
- a, stigma; b, upper half of the upper anther; c, lower half of the upper anther connected with the upper half of the lower; d, lower half of the lower anther; e, style.

pathfinders. As in *Odontites serotina*, the pollen is smooth and powdery, and falls on the head or proboscis of the visitor; but the details of the process by which the pollen is scattered are unlike those of the former species. While in *Odontites serotina* the anthers are only held together posteriorly by matted hairs, in *E. officinalis* the lower anther-lobe of the upper stamen on each side coheres with the upper anther-lobe of the lower; and the two superior anthers further cohere firmly together. Another peculiarity is directly connected with this. While in *Odontites serotina*

all the anther-lobes end alike in short points, in *E. officinalis* the upper lobe of each anther is blunt, but the lower is provided with a thin, stiff spine (3, Fig. 154). Of these four spines it is almost exclusively the two lower ones that come in contact with insects; for not only are they much longer than the upper ones, but the stamens which bear them are inclined at an angle of about  $60^\circ$  from the upper pair, and their anthers bend downwards so much that the spines stand well down in the mouth of the flower (1, Fig. 154). In *Odontites scrotina* the pointed anther-lobes must themselves be touched for the pollen to be shaken out, and the broad filaments, placed close together and set with sharp points on their inner side, insure this. In *E. officinalis*, on the other hand, it is sufficient if one of the long spines on the lower anthers be touched, and accordingly the filaments curve widely apart, standing close to the wall of the corolla; and they are smooth and narrow, so that an insect can insert its head into the tube without hindrance. In doing so it touches the lower anther-spines, and shakes the whole system of anthers, causing the pollen to fall out. Rows of hairs on the upper anther-lobes prevent the pollen from being scattered at the sides, and insure its falling on the head of the insect.

In the points described hitherto all my specimens of *E. officinalis* agree with one another. But in regard to the size and conspicuousness of the flowers, and the possibility of self-fertilisation, I have found two different forms of this plant—one large-flowered, which never fertilises itself, and one small-flowered, which in absence of insects fertilises itself regularly. Intermediate forms may probably occur, but were not present among my specimens.

In the large-flowered form (4, Fig. 154), probably *E. montana*, Jord., the stigma protrudes from the flower before the anthers are ripe, and even after the anthers are ripe it is the first part to be touched by insect-visitors, and is, therefore, regularly cross-fertilised; in absence of insects, it is incapable of self-fertilisation.

In the small-flowered form, probably *E. gracilis*, Jord. (1, Fig. 154), when the flower opens, the stigma stands so far above and behind the anthers that it escapes being touched by insects; the style gradually elongates and carries the stigma downwards and forwards into a position where it will be touched before the anthers by an insect's head, and where, in absence of insects, pollen can fall from the upper anthers upon it.

Thus in case of insect-visits cross-fertilisation is insured in both forms, but in absence of insects self-fertilisation is only possible in the small-flowered plants.

Delpino (178) seems to have examined the large-flowered form only, and Axell (17) the small-flowered; for the former describes *E. officinalis* as proterogynous, and the latter as proterandrous.

Visitors: A. Hymenoptera—*Apidæ*: (1) *Bombus agrorum*, F. ♀; (2) *B. pratorum*, L. ♀; (3) *Apis mellifica*, L. ♀; (4) *Nomada lateralis*, Pz. ♀, all s. B. Diptera—(a) *Bombylidæ*: (5) *Systæchus sulfureus*, Mik. (Sld.); (b) *Syrphidæ*: (6) *Syrphus* sp.; (7) *Melithreptus tæniatus*, Mgn., all s. Additional lists of visitors to the large-flowered form are given in No. 590, III., and No. 609.

*Euphrasia salisburgensis*, Funck.—The flowers resemble in size the small-flowered form of *E. officinalis*, and their arrangements for cross-fertilisation resemble the large-flowered form of that species. The corolla continues to grow, carrying forward the stamens after the style has stopped growing, and in absence of insects self-fertilisation takes place in the end. The visitors are bees and Lepidoptera (609).

333. *PEDICULARIS SILVATICA*, L.—In this plant, as in *Rhinanthus* and *Melampyrum*, the opposite pairs of anthers lie with their edges close together,—and all four unite to form a quadrangular pollen-receptacle (3, Fig. 155) which is inclosed in the hooded upper lip. The mechanism by which pollen is shed upon the insect-visitor is here more complex and more rich in adaptations than ever, and more difficult to understand in its details without direct observation of its action. Sprengel (702) and Hildebrand (346), neither of whom observed insects in the act of fertilising the flower, have very naturally overlooked many of its most interesting adaptations. Dr. Ogle (632), who watched the flowers in the open air and saw them visited by humble-bees, gives an accurate account of the process of cross-fertilisation; but many adaptations have escaped even his notice, and some he has interpreted wrongly. It is therefore still worth while to describe the whole structure of the flower minutely.

Honey is secreted by the green, fleshy base of the ovary, and lies at the bottom of the tube, which is 10 to 14 mm. long, laterally compressed, and so narrow that a humble-bee can only insert the forepart of its head. At the height of 10 to 14 mm. the tube divides into an upper lip, which both in form and in direction is simply a continuation of the tube, slightly wider and open in front, and an under lip, whose base (3 to 5 mm. long) is applied to the upper lip so as to close up the lower 3 to 5 mm. of the

mouth of the flower. The hooded end of the upper lip incloses the stamens, and the end of the style with the stigma protrudes obliquely downwards from it; the free portion of the under lip with its three lobes serves as a standing-place for insects, and is set very obliquely, so that the right lobe stands 2 to 8 mm. higher

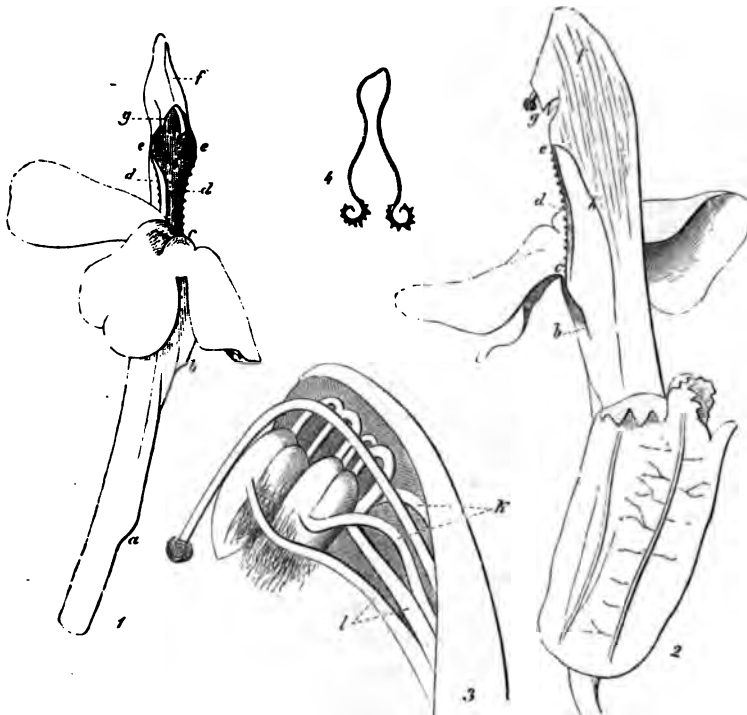


FIG. 155.—*Pedicularis silvatica*, L.

- 1.—Corolla, from the front.
  - 2.—Flower, from behind.
  - 3.—Upper part of the corolla, from the left side. The left half of the corolla has been cut away, and the anthers have been pushed asunder.
  - 4.—Transverse section of the corolla at *c*, 1, 2. (1—3,  $\times 3\frac{1}{2}$ ; 4,  $\times 7$ .)
- a*, point of insertion of the anterior stamens; *b*, point of origin of the lower lip; *b c*, lower part of the mouth of the flower, closed by the apposition of the lower lip; *d*, revolute edge of the upper lip, set with teeth; *e*, widest part of the mouth into which the bee inserts its head and proboscis; *f*, the hood which surrounds the anthers; *g*, pendulous tip of the hood; *h*, ridge upon the side of the corolla, meeting the revolute border at *e*; *k*, shorter, *l*, longer stamens.

than the left (1, Fig. 155). If the under lip is pulled down as far as the place of its attachment, the mouth of the flower is seen to form a fissure 8 to 10 mm. long, which in the greater part of its length is only 1 to 2 mm. broad, but which 3 mm. below its upper end widens out suddenly to a breadth of 4 mm. (*e*, *e*, 1); it then

again narrows suddenly, and a little more than 1 mm. from its upper end two sharp processes of the hood (*g*, 1, 2) almost meet in the middle and divide the entrance into a very small upper and a long lower part. Through the upper opening protrudes the style, which springing from the bilocular ovary lies close to the posterior wall of the corolla, and curves sharply downwards near its anterior end to bear the capitate stigma; the long, lower opening admits the bee's head. So long as this slit is only 1 to 2 mm. broad, viz., from the insertion of the under lip to the wider part above, its edges are very markedly rolled outwards, and that part of the inner wall of the corolla which is brought by this evolution of the edge to form the margin of the narrow slit is closely set with sharp points (*d*, 1, 2, 4), while the wider portion (*e*, 1) has smooth edges. There is also on each side of the upper lip a reddish thickened band (*h*, 2), which begins on a level with the wide part of the slit at the upper end of the evolved edges (*e*), and forming a sharp angle with the ridge runs backwards and downwards to disappear on a level with the base of the under lip.

What have all these characters, the compressed base of the under lip, the oblique position of its three-lobed lamina, the evolved edge of the narrow entrance, its rough edges, the sudden enlargement with its smooth edges, the red stripes at the sides of the upper lip, to do with fertilisation by humble-bees? Are they accidents to be neglected, as is done by Hildebrand in his figures in the *Botanische Zeitung* (1866, pl. iv.) and by Dr. Ogle in the *Popular Science Review* (Jan. 1870)? Careful observation of an insect visiting the flower makes me think otherwise. The bee comes flying along with outstretched proboscis, and avoiding the toothed edges of the slit, thrusts its proboscis at once in alighting into the widest part of the opening (*e*, 1); the upper part of its head then touches the stigma, which stands scarcely 2 mm. above the wide part of the opening, and the oblique position of the lower lip causes the bee's head also to be placed obliquely; its forefeet grasp the basal part of the lower lip, its middle pair of feet grasp the tube of the flower on a level with the lower lip, and the hindfeet rest upon leaves or other flowers below. Standing in this position, the bee applies its head, which is  $2\frac{1}{2}$  to 3 mm. thick and 5 mm. broad, to the (4 mm.) wide part of the entrance, with just so much obliquity as gives it the best chance of entering. And now the edges of the slit, rolled outwards and thereby stiffened (*d*, 1, 2), and the bands on the upper lip (*h*, 2), play their part. Joining above at a sharp angle, they bound, on each side of the

upper lip, a triangular surface, which does not bend, but gets pushed outwards by the bee's head. But the points where the evolute edges and the thickened bands meet are on each side of the wide part of the opening, and as they separate more and more from one another, the superior angle (*e, g, e, 1*) of the small part of the entrance above this will be very greatly enlarged, for the sides bounding it are very short, and are forced apart as much as the long sides of the lower opening. The small processes (*g, 1, 2*) which before nearly met, and which held together the two halves of the pollen-receptacle, are forced apart; the anthers, which have a tension outwards in consequence of the peculiar curvature of their filaments (*k, l, 3*),<sup>1</sup> are freed from the force that held them together below, while they remain fastened together above; they therefore flap apart, and let a little pollen fall on the bee's head, exactly on the spot which came in contact with the stigma scarce a second before. The pollen is saved from being scattered at the sides by vertical hairs on the longer stamens (*l, 3*),<sup>2</sup> which cover the space between the upper and lower anthers on each side, and project slightly beyond the lower edges.

*Bombus hortorum*, L. ♀ (20 to 21 mm.), needs to thrust its head a very little way down after inserting it into the wide entrance; but the shorter a bee's proboscis is the more must it force its head down in the upper lip, and if there is not space enough *above* the platform of the lower lip, the latter can be pressed down 3 to 4 mm., as far as *b, 2*; so that bees with a proboscis only 10 mm. long may reach the honey. When the bee flies away, the lower lip springs back into its former position, and the whole mouth of the flower resumes its original state.

The flower is in this way adapted for all our native species of *Bombus* and *Anthophora*, except *B. terrestris* and small workers of a few other species; but the length of the tube excludes all smaller bees, which if the tube were shorter might carry off the honey without touching the stigma; the hooded upper lip guards the pollen from flies and other insects; but the tube is liable to be bitten through and robbed of its honey by some humble-bees.<sup>3</sup> Such robbery does little or no harm, for bees still visit

<sup>1</sup> I have never noticed the anthers adhering at all to the inner surface of the corolla, as Dr. Ogle describes. Such an adhesion, if it exists, must be very slight indeed.

<sup>2</sup> According to Dr. Ogle (No. 632, p. 46), the lower anthers are held together by the pressure of these hairs upon the wall of the corolla. To act in this way the hairs would have to be directed obliquely outwards. They are not so, but lie parallel to the median vertical plane of the flower.

<sup>3</sup> Dr. Ogle is mistaken in thinking (No. 632, p. 180) that the wide calyx is sufficient to protect *Pedicularis silvatica* from robbery on the part of short-tongued bee

in a legitimate manner flowers which have been bitten through and robbed.

The power of self-fertilisation has been completely lost.

Visitors: Hymenoptera—*Apidæ*: (1) *Anthophora retusa*, L. ♂ (16—17); (2) *Bombus hortorum*, L. ♀ (20—21); (3) *B. agrorum*, F. (12—15); (4) *B. lapidarius*, L. ♀ (12—14); (5) *B. silvarum*, L. ♀ (12—14); (6) *B. Scrimshiranus*, L. ♀ (10), all sucking normally, very ab.,—*B. Scrimshiranus*, L. ♀ (9), bites through the corolla close above the calyx, and so reaches the honey; (7) *B. terrestris*, L. ♀ (7—9), very ab., only reaching the honey by biting,—once I saw it gnawing the upper lip, above the anthers.

*Pedicularis rostrata*, L., *P. verticillata*, L., *P. tuberosa*, L., were seen by Ricca to be visited by humble bees (665). On the Alps, I have observed in addition to these three species, *P. palustris*, L., *P. recutita*, L., *P. asplenifolia*, Floerke, and *P. foliosa*, L. (609). In *P. verticillata*, the calyx is swollen, and the lower part of the corolla-tube is bent at right angles within the calyx; the honey is thus guarded from *Bombus mastrucatus*, which tries in vain to reach it, and which frequently bites through the tubes of *P. tuberosa* and *P. foliosa*, etc.

The six species of *Pedicularis* which grow in Nova Zembla are all fertilised, in Delpino's opinion, by *Bombus terrestris*, and so also is *P. Kanei*, which is found in lat. 79°, on the west coast of Greenland (172, 352). If this is really the case, all these species must have a shorter tube than *P. silvatica*.

334. RHINANTHUS CRISTA-GALLI, L.—In this plant, as in the foregoing, the dry smooth pollen is shed on the insect's head, but the details of the mechanism are very different. Each anther lies so close to its opposite neighbour, and they dehisce so widely on their opposed faces, that both together form one pollen-reservoir, closed in by matted hairs with which the contiguous edges of the anthers are provided (1, 2, Fig. 156). These pollen-reservoirs are borne on stiff filaments, of which the anterior pair are close together at their bases, and are beset with sharp points on their inner sides (1) so that a bee cannot insert its proboscis there; higher up, for the space of a few millimetres below the anthers, they are smooth and wide enough apart to admit the point of a bee's proboscis easily. As soon, however, as the bee pushes its proboscis farther in, it forces the filaments apart, and tears asunder the two halves of the pollen-reservoir. The pollen falls out on to the bee's proboscis, and is prevented from being scattered at the sides by the fringe of hairs on the lower edge of the anthers. This pollen-mechanism is

better protected than in the foregoing species, for the helmet-shaped, laterally compressed upper lip covers it both above and at the sides, and at first leaves only a narrow slit, which is slightly more dilated just below the anthers to admit the bee's proboscis. Honey is not secreted by the ovary itself, but by a development of the receptacle, which is prolonged downwards and forwards into a long, fleshy lobe, turned up at the edges (*n*, 4). As in *Euphrasia officinalis*, so also in this plant, two different forms exist,<sup>1</sup> one inconspicuous and regularly self-fertilising, the other more conspicuous

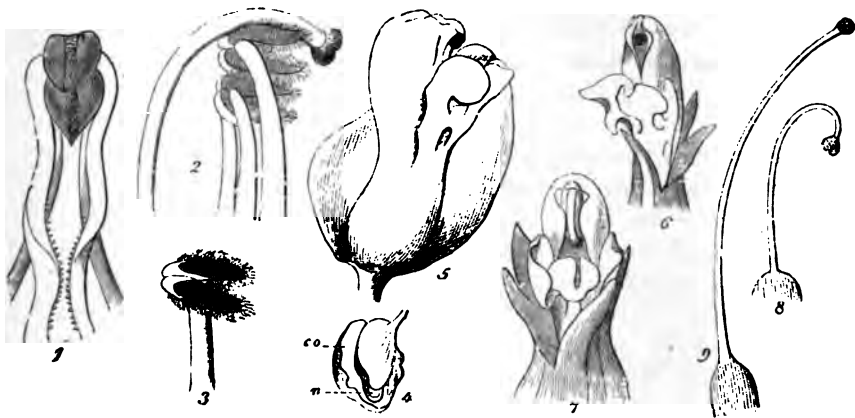


FIG. 156.—*Echinanthus crista-galli*, L.

- 1.—Anthers, from the front.
  - 2.—Ditto, with the style, from the side.
  - 3.—An anther, from the inner side.
  - 4.—Ovary, with the base of the style, nectary (*n*), and base of the corolla (*co*).
  - 5.—Flower, of the variety *minor*, after removal of the right half of the calyx, from the side.
  - 6.—Upper part of ditto, at the beginning of the flowering period, from the front.
  - 7.—Ditto, at the end of the flowering period.
  - 8.—Style of the variety *minor*.
  - 9.—Style of the variety *major*.
- (1—3,  $\times 7$ ; 4—9,  $\times 8\frac{1}{2}$ .)

and incapable of self-fertilisation. Delpino, who has thoroughly described the mechanism of this flower, has only had the larger form (*major*) under examination; for he calls Vaucher's fairly accurate account (752) of the occurrence of self-fertilisation, merely a product of the imagination.<sup>2</sup>

*R. minor*, Ehrh.—In the small-flowered form, the tube, whose base contains the honey, is 7 to 8 mm. long, so that the honey is

<sup>1</sup> Linnæus distinguished these as varieties ( $\alpha$  and  $\beta$ ). Later authors have advanced them to the rank of species, *R. major*, Ehrh., and *R. minor*, Ehrh.

<sup>2</sup> No. 178, p. 183, "Ora tutto ciò non è che un parto della immaginazione."

accessible to all our humble-bees, the shortest proboscis among which, that of *B. terrestris*, is 7 to 9 mm. long. The mouth of the corolla is a slit 6 to 7 mm. long, which, however, is reduced to 4 mm. by the position of the upper lip. The remaining posterior part of the slit is blocked by the stamens in the manner already described, so that the bee can only insert its proboscis beneath the anthers. The stigma curves down so far over the anthers (6, Fig. 156) that an insect's proboscis must touch it before entering further and being dusted with pollen. In general, however, bees' visits are scarce; for the corolla is almost inclosed in the vesicular calyx, and is therefore inconspicuous. In absence of insects, self-fertilisation always takes place; for the mouth of the corolla gradually opens more widely, the under lip bending downwards, and the sides of the upper lip spreading further apart (7, Fig. 156); at the same time the style elongates and curves downwards and inwards (7, 8), so that the stigma comes to stand under the anthers, or even between them if they have separated in withering.

*R. major*, Ehrh.—In the large-flowered form, the tube is about 2 mm. longer than in the small-flowered; but this small difference suffices to exclude many of our humble-bees from the honey, or to cause them to bite a hole in order to gain access to it. Sprengel observed these holes, but they are not made, as he said, by "a large humble-bee, for whom the natural entrance is too small," for all humble-bees insert only their proboscis into the flower; but by those with the shortest proboscides, namely, as I have repeatedly observed, by *B. terrestris*, L. ♀ and ♂, and *B. pratorum*, L. ♂, whose proboscides measure respectively 7 to 9 mm. and 8 mm.

The size of the parts projecting beyond the calyx, viz. the upper and lower lips, differs more than the length of the tubes in the two varieties or sub-species. The upper lip is in *R. minor* 7 to 8 mm., in *R. major* 10 to 11 mm. long. The flowers of *R. major* are therefore more conspicuous, and their conspicuousness is increased by the pale colour of the bracts and by the violet colour of the tip of the upper lip, which is usually white in *R. minor*. As both species grow together in the same spots and flower at the same time, they give a good opportunity of proving that the large-flowered form is really much more plentifully visited than the other. In point of fact, insect-visits are so plentiful in the case of *R. major*, that it has been able to dispense with the power of self-fertilisation, and the style, instead of bending downwards, projects more and more from the mouth of the flower.

We have thus in *Rhinanthus major* and *minor* two forms

engaged in the struggle for existence;<sup>1</sup> the one excels in conspicuousness and the abundance of its insect-visitors, the other in its power of self-fertilisation. The former seems to have the advantage, for both in Westphalia and, according to Ascherson's *Flora*, in Brandenburg it is much more plentiful than the smaller form; it is also more plentiful both in England and Ireland according to Mr. T. H. Corry.

The following list includes the visitors to both forms:—

(1) *Bombus* (*Apathus*) *Barbutellus*, K. ♀ (12); (2) *B. Rajellus*, Ill. ♀ (12—13); (3) *B. hortorum*, L. ♀ ♂ (19—21); (4) *B. silvarum*, L. ♀ ♂ (10—14); (5) *B. senilis*, Sm. ♀ ♂ (14—15); (6) *B. Scrimshiranus*, K. ♀ (10); (7) *B. hypnorum*, L. ♀ (10—12), all only sucking normally; (8) *B. terrestris*, L. ♀ ♂ (7—9), (9) *B. pratorum*, L. ♀ (8), both sucking normally on *R. minor*, but obtaining the honey of *R. major* by biting a hole in the spur.

Several of the above-named humble-bees were caught carrying *Rhinanthus* pollen in their collecting-baskets,—viz. *B. terrestris*, ♀ ♂, and in especial numbers (in the Hoppekethal, July 11, 1869), *B. hypnorum*, ♀, and *B. pratorum*, ♀. Sprengel mentions the honey-bee as a frequent visitor, but I have never observed it; its proboscis (6 mm. long) is at any rate too short to reach the honey in the legitimate manner.

I have seen one of the Noctuidæ, *Euclidia glyphica*, L., repeatedly sucking the honey of this flower; but the tongues of Lepidoptera are so thin that they can reach the honey without pushing the anthers apart, and Lepidoptera therefore are quite useless to the plant.

In *Rhinanthus Alectorolophus*, Poll.,<sup>2</sup> we have an intermediate stage between *R. crista-galli* and *R. alpinus*. The corolla is produced into a beak-like prolongation close under the projecting stigma, and above the entrance made use of by bees; this process of the corolla bears a small opening, bounded by two blue lobes. This small opening permits Lepidoptera to insert their thin tongues, which touch first the stigma and then the anthers; and as a matter of fact this species is visited and cross-fertilised both by Lepidoptera and by humble-bees (570, 609).

In *Rhinanthus alpinus*, Brng., the lower or bees' entrance is closed, its edges coming close together without uniting, and only the small upper opening remains; and this species is therefore

<sup>1</sup> Compare *Malva rotundifolia* and *M. silvestris*, p. 142.

<sup>2</sup> Included by Nyman, *Conspectus Floræ Europææ*, under *R. major*.

anthers lie well in front of the stigma

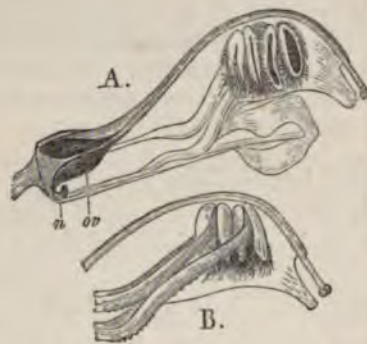


FIG. 157.—*Rhinanthus Alektor*

A.—Flower, in longitudinal section, after removal of  
 B.—Upper part of a flower, from which the right half  
 C.—Ditto, viewed from the front.  
 D.—Ditto, after removal of the lower lip. ( $\times 3\frac{1}{2}$ .)  
 hth, aperture for humble-bee's proboscis; fth, aperture  
 n, nectary; ov, ovary; st, stigma.  
 (St. Gertrud, July 22, 1875).

335. MELAMPYRUM PRATENSE, L.—  
 the pollen is shed in *Melampyrum* is a  
 foregoing; for here all the four anthers  
 a single pollen-reservoir, which is open  
 appendage borne by each anther-lobe.  
 other remarkable peculiarities. Honey

5 mm., the tube is so wide that a humble-bee's head enters it easily; a proboscis 10 to 11 mm. long therefore suffices, and only *B. terrestris* and small workers of some other species are excluded.

In its narrower part the tube is three-sided, the lower wall standing horizontal, the sides first bending sharply inwards then rising almost perpendicularly, and holding the style in their upper angle. All three sides widen out gradually for a space of 8 to 10 mm. from the base of the tube, then, on a sudden, more rapidly, the sides rising up into a hood for the pollen-reservoir, and the floor increasing from 3 mm. to 5 mm. in breadth. In this wide part of the tube the lower part of the side walls is doubled down upon the floor by a re-entrant fold (*a*, 2, 3), so that the breadth of the entrance is reduced to scarcely 3 mm.; and this is further reduced in height to 1 to 2 mm. by two dark-yellow pouches in the under lip (*pathfinders*, *b*, 3), and by a fold close behind the free edge of the hood-like upper lip; if, however, the folds in the side walls and in the upper lip are opened out by a bee thrusting in its head, there is plenty of room in the broad part of the tube for the bee's head, which is about 5 mm. broad, and 3 mm. high. So by this peculiar conformation of the mouth, weak, short-lipped insects are excluded, and at the same time humble-bees are permitted to insert their heads. There are yet other peculiarities in the mouth of the flower which complete this result. The filaments which, in the narrow part of the tube, are thin and adhere to the corolla, become free from it in the wide part, and rise obliquely upwards as stiff, broad rods beset with teeth on their inner sides, towards the hooded upper lip, which incloses the stamens. The two anterior stamens lie, in their ascending portions, so close behind the entrance of the flower that they block it for a further space of  $\frac{1}{2}$  mm. on either side. So in looking from the front into the mouth of the flower we see an opening only 2 mm. broad and scarcely so high, bounded on the right and left by the prickly margins of the filaments, above by the soft tufts of hairs on the upper lip, and by the weak hairs projecting downwards from the pollen-receptacle (*d*, 3). The bee in inserting the delicate tip of its proboscis carefully avoids any rough contact; therefore, in this flower, it directs it neither to the right or left, where it would meet the sharp points upon the stamens, but upwards where it rubs against the soft hairs of the upper lip and the pollen-receptacle in passing into the tube. This course is essential for cross-fertilisation.

The style traverses the upper angle of the tube in its whole length, and bends down with it over the pollen-receptacle, so that its stigmatic end hangs down in the upper part of the mouth of the flower between the tufts on the upper lip, and is thus inevitably touched by the bee's proboscis as it enters. The four

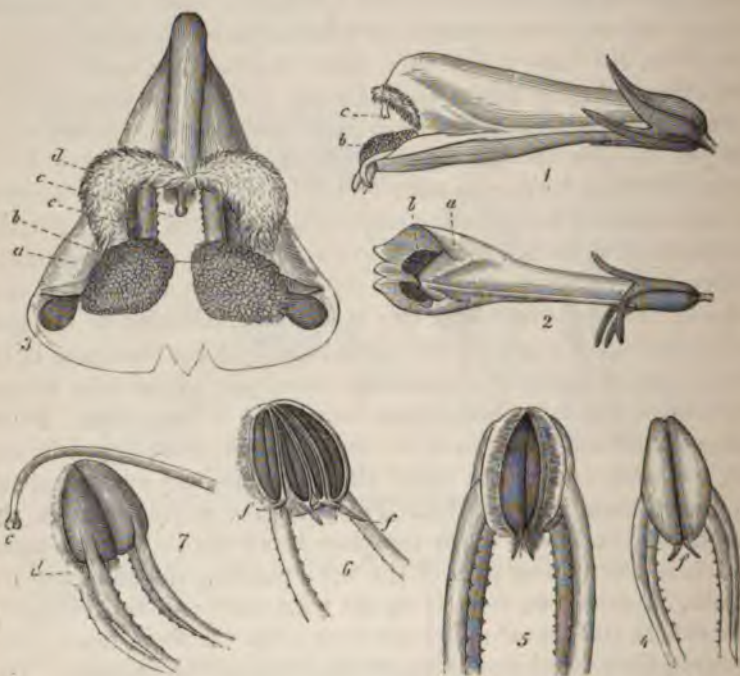


FIG. 158.—*Melampyrum pratense*, L.

- 1.—Flower, from the side ( $\times 3$ ).
  - 2.—Ditto, from above.
  - 3.—Ditto, from the front ( $\times 7$ ).
  - 4.—The pollen-receptacle formed by the anthers, viewed from behind.
  - 5.—Ditto, after it has opened, from before.
  - 6.—The two anthers of the right half of the flower, seen from the left.
  - 7.—Relative positions of pollen-receptacle and stigma.
- a, side-fold in the forepart of the corolla; b, pathfinder; c, stigma; d, hairs of the pollen receptacle; e, teeth upon the filaments; f, appendages of the anthers.

pairs of anther-lobes, which have stiff walls and are in firm connection with the stiff filaments, cohere closely by their upper and posterior edges, but admit of some motion at their lower and anterior edges, which are fringed with hairs. Each anther-lobe is prolonged downwards into a stiff, sharp process, so that four pairs of these sharp processes point downwards; of these

the hindmost are the longest, as they might easily escape being touched if of the same length with the others. The bee's proboscis, entering the flower in the way described above, comes in contact immediately afterwards with the sharp processes of the anthers; the anther-lobes at once separate slightly at their lower and anterior edges, and the fine, dusty pollen is shed upon the insect's proboscis.

In spite of these manifold adaptations, the plant, from growing in shady spots, is, as a rule, sparingly visited by bees; but in their absence self-fertilisation takes place regularly. As in *Rhinanthus minor*, the end of the style curves more and more downwards, and at last inwards, so that the stigma comes to lie below the pollen-receptacle (5, Fig. 158), which in the old flower opens of itself. In flowers whose colour has changed to reddish the stigma is always found in this position.

Visitors: Hymenoptera—*Apidae*: (1) *Bombus agrorum*, F. ♀ ♀! (10—15), sucking normally. Its weight bends down the flowers to which it hangs. It first inserts the tip of its proboscis into the upper part of the flower, then thrusts the whole proboscis and its head into the tube. After visiting a flower, which takes only a few seconds, it almost always flies away to a neighbouring plant. (2) *B. hortorum*, L. ♀! (18—20), sucking normally, just as the former species (Siebengebirge, July 8, 1871); (3) *B. terrestris*, L. ♀ (7—9), bites through the corolla close above the calyx, so that one mandible makes a hole on each side of the sharp edge of the corolla, and through one of these two holes the bee inserts its proboscis; (4) *B. pratorum*, L. ♀ ♂ (8—9), acts similarly (Siebengebirge, July 8, 1871); (5) *Apis mellifica*, L. ♀ (6), do., very ab.; (6) *Megachile circumcincta*, K. ♀! (11), sucking normally, only one specimen. B. Diptera—*Stratiomyidae*: (7) *Oxycera pulchella*, Mgn., I saw this species on the flowers at Warstein,—it probably could not reach either the honey or the pollen. See also No. 590, III.

*Melampyrum arvense*, L., is visited by various insects, but only fertilised by very long-tongued humble-bees (590, III.).

*Melampyrum nemorosum*, L.—The honey is stolen by various humble-bees, but the flower is fertilised only by *Bombus hortorum*, L. ♀ (590, III.).

*Melampyrum silvaticum*, L.—The flower is of small size and its mechanism is much simplified (590, III.).

The six forms above described in which dry pollen is shed on the insect-visitor, viz. *Odontites lutca*, *O. serotina*, *Euphrasia officinalis*, *Melampyrum*, *Rhinanthus*, and *Pedicularis*, show remarkable gradations in the way in which the anthers are protected and the

pollen lodged, and in the mechanism for scattering the pollen and for guiding the insect's proboscis.

*a.* The protection of the anthers. In *Odontites lutea* the anthers protrude from the flower, as in *Veronica*; in *Odontites serotina* they are only slightly covered by the upper lip, while they are entirely covered by it in *E. officinalis*; in the three others they are completely inclosed in the hood of the upper lip.

*b.* The pollen-receptacles. In the two species of *Odontites* and in *Euphrasia officinalis* each anther-lobe forms a separate receptacle opening at the apex; in *O. lutea* all the anthers are separate; in *O. serotina* they are connected posteriorly by matted hairs; in *E. officinalis* their edges cohere. In *Melampyrum*, *Rhinanthus*, and *Pedicularis*, their edges are closely united so as to form a single, more or less distinctly four-chambered receptacle.

*c.* The shedding of the pollen. In *O. lutea* and *O. serotina* the anthers must be touched in order to shed their pollen; in *O. lutea* each must be touched separately, but in *O. serotina* one touch is communicated to all. In *E. officinalis* the lower anthers, in *Melampyrum* all of them, bear sharp appendages which point downwards, and which, when touched, cause the pollen to fall out. In *Rhinanthus*, the pollen-receptacle is opened by pushing apart the filaments. In *Pedicularis*, the edges of the hood which incloses the pollen-receptacle are separated by a complex system of levers, and the pollen-receptacle then opens. In all, except *O. lutea*, hairs directed downwards (either from the edges of the anthers or from the filaments) prevent the pollen being scattered at the sides.

*d.* The path of the bee's proboscis. In *O. lutea* and *E. officinalis* the path is only marked out by the entrance of the tube; but in *O. lutea* the bee's proboscis cannot fail to come in contact with one or other of the anthers, and in *E. officinalis* with their appendages. In the other four species sharp points on the filaments or on the edges of the upper lip cause the bee to insert the tip of its proboscis just in such a position that it may first touch the stigma and then dust itself with pollen.

In regard to all four characters *Odontites lutea* stands lowest, and *Pedicularis silvatica* highest.

Cross-fertilisation in case of insect-visits is insured in all the six species by the stigma being touched in all or most flowers by the same part of the insect which is immediately afterwards dusted with pollen. In three species out of the six, two forms of flowers occur, of which one is sparingly visited by insects and in

their absence fertilises itself regularly, and the other is abundantly visited by insects and is incapable of self-fertilisation. In *Euphrasia officinalis* and *Rhinanthus crista-galli* it is the small-flowered form, in *Odontites serotina* it is the plants inhabiting shady places, which receive so few insect-visits that self-fertilisation becomes necessary; in *Melampyrum* and *Odontites lutea* self-fertilisation occurs in absence of insects, but in all flowers without distinction; in *Pedicularis silvatica* alone, the conspicuousness of the flowers and the perfection of the pollen-apparatus insures cross-fertilisation so well that self-fertilisation never takes place.

The section of the Scrophularineæ characterised by a pollen-distributing mechanism is remarkable also for the gradations in the development of its nectaries. Usually part of an organ already present secretes honey, especially the lower part of the outer wall of the ovary, which sometimes secretes its honey all round (*Tozzia*), sometimes mainly or solely in front (*Euphrasia* and *Odontites*). With the growth of this new function the secreting tissue thickens and forms a protuberance scarcely noticeable in *Euphrasia minima*, but evident in *E. salisburgensis* and *Pedicularis asplenifolia*, Fl.; it becomes a strongly marked swelling in *P. verticillata*, L., and *P. recutita*, L., which in *P. palustris*, L., is more sharply marked off from the ovary, and in *Rhinanthus* becomes a cup extending forwards from the base of the ovary, which contains the nectar, and is most perfectly developed in *R. alpinus*. We thus have a complete series of transitions, from secretion of honey by an organ whose proper function is quite different, to the development of a special nectary.

#### REVIEW OF THE SCROPHULARINEÆ.

The Scrophularineæ described above may be arranged in four groups according to their pollen-distributing mechanism and the insects which fertilise them.

1. *Verbascum* and *Veronica* have open flowers, with short tubes and freely exposed reproductive organs which insect-visitors may come in contact with at any part, though they as a rule touch the stigma before the anthers. Only in some *Veronicas*, especially in *V. Chamædrys*, the filaments by spreading apart and thinning away

at the base form a delicate pollen-distributing apparatus. The fertilisers are flies and bees.

2. *Scrophularia* has short, round, brownish flowers, with a widely open mouth and easily visible honey. The stigma ripens before the anthers, and both come in contact inferiorly with the insects. Wasps are the chief fertilisers.

3. *Digitalis*, *Antirrhinum*, and *Linaria* have long and wide tubes, open in *Digitalis* and closed in the other two. The insect-visitor creeps entirely or almost entirely into the tube, and touches anthers and stigma with its back. The fertilising-agents are large bees.

4. *Euphrasia*, *Odontites*, *Rhinanthus*, *Melampyrum*, and *Pedicularis* have narrow tubes which divide into an upper lip protecting the anthers, and a lower lip serving as a platform for insects to alight on. They dust their insect-visitors with smooth, powdery pollen. The forms with shorter tubes are fertilised by bees and flies, those with longer tubes almost exclusively by humble-bees.

On the Alps we have in addition *Tozzia*, fertilised by flies, *Rhinanthus Alectorolophus* by humble-bees and Lepidoptera, and *R. alpinus* by Lepidoptera (609).

In almost all the Scrophularineæ that we have considered, cross-fertilisation is effected by the stigma being touched before the stamens or pollen-apparatus by insect-visitors; but in some cases dichogamy also occurs. In default of insect-visits, self-fertilisation takes place in most forms; and only in a few are insect-visits, and consequently cross-fertilisation, so far insured that self-fertilisation is never required and has become impossible.

This family affords another instance of the association of certain colours with fertilisation by certain insects. In the section characterised by loose dry pollen, the lowest forms (*Tozzia*, *Odontites lutea*, and *Euphrasia minima*) are all yellow, while in the highest (*Melampyrum*, *Pedicularis*) red and purple colours appear. The uncommon colour of *Scrophularia* must be referred to the peculiar taste of its visitors, the wasps. The colours of the genus *Veronica*, which is fertilised by flies, remain to be explained. Most species have light or dark blue flowers; those of *V. urticifolia*, and *V. peregrina*, L., are pink. In spite of its apparently simple flower, *Veronica* is by no means a primitive form among the Scrophularineæ: the symmetrical flower, the specially differentiated nectary, the reduction of the sepals and petals to four, and of the stamens to two, are all characters widely removed from the primitive type. The short-tubed species of *Veronica* must be

looked upon as the more primitive, from which the long-tubed type of *V. spicata* has been evolved by the agency of bees and sand-wasps. Two different hypotheses suggest themselves for the origin of the genus *Veronica*. In the first place, the reduction of the stamens to two may be due to the development of the delicate pollen-shedding mechanism adapted for Syrphidæ, which we found to be best developed in *V. Chamædrys* and *V. urticifolia*; just as in *Salvia* two stamens have certainly become aborted owing to the development of the special lever-apparatus in the others. According to this view, the oldest Veronicas are those which are adapted for Syrphidæ, the others, with short tube and flat limb, being developed from them by degeneration of the pollen-mechanism; and several species (e.g., *V. Beccabunga* and *V. aphylla*) do seem to show such a degeneration. But it is conceivable that the ancestors of *Veronica* suffered reduction in the number of their stamens simply in consequence of gradual diminution in size, as in *Lycopus* among Labiates, several *Saginæ* among Alsineæ, small-flowered species of *Ranunculus*, *Chasalea*, and the small-flowered form of *Stellaria media*, L.; and that the pollen-mechanism was subsequently developed in one section of the genus. In this case we must ascribe to a miscellaneous lot of Syrphidæ and small bees the blue colour of the simpler Veronicas which are not provided with any special adaptations for Syrphidæ; for the Muscidæ and other Diptera, which also visit and fertilise these simpler Veronicas, show no signs of favouring the production of a blue colour in any other instance. I see as yet no grounds for preferring either of these hypotheses to the other.

#### ORD. LENTIBULARIÆ.

*Utricularia*, L.—Buchenau has investigated thoroughly the structure and development of the flower.<sup>1</sup> Hildebrand has explained the mechanism of fertilisation (356). An insect, thrusting its proboscis beneath the upper lip to reach the honey contained in the spur, first touches with its back one of the stigmatic lobes, which project beyond the anthers and have their papillar surfaces directed downwards; immediately afterwards it comes in contact with the anthers and gets dusted with fresh pollen. The stigma is irritable, folding upwards at once on being touched, so that pollen cannot be applied to the stigma of the same flower as the insect draws back.

<sup>1</sup> *Botan. Zeitung*, 1865, p. 63.

*Pinguicula alpina*, L.—The structure of the flower is similar, but the stigma, instead of folding up by its own irritability, is pushed upwards by the retreating insect (Hildebrand, 356). A fly, forcing its way into the pale yellow flower, rubs against the stigma with its back and dusts it with pollen from another flower. It now tries to move upwards, as far as possible, to free itself from certain stiff hairs directed obliquely backwards on the inferior wall of the corolla, and in doing so it dusts its back with fresh pollen (589, p. 334; 609). Some flies, which are large enough to get caught firmly but not strong enough to make their escape, are held fast and perish.

*Pinguicula lusitanica*, L., is self-fertilising (Henslow).

*Pinguicula vulgaris*, L.—Axell gives a figure and description of the flower, which agree with Hildebrand's account (17). This species is adapted for bees (609).

#### ORD. GESNERACEÆ.

The flowers are markedly proterandrous (172, 178, 632).

#### ORD. BIGNONIACEÆ.

*Bignonia*, L.—The flowers are proterandrous. The lobes of the stigma are touched first by an insect-visitor, and therefore get dusted with pollen from a previously-visited flower; they then close up immediately, before pollen from their own flower can reach them (178).

*Martynia*, L. (Pedalineæ), has a similar arrangement (172, 352).

My brother Fritz Müller fertilised a species of *Bignonia* (*Cipo alho* of the Brazilians) in South Brazil as follows:—

(1) Twenty-nine flowers on two stocks with pollen of their own stock; all fell off in a short time.

(2) Thirty flowers on the same two stocks with pollen from others growing near by; only two flowers developed fully, but most remained longer upon the stem than in the previous case, and many showed a commencing enlargement of the ovary.

(3) Five flowers on one stock with pollen from another growing at a distance; all five were fruitful (551).

*Tecoma capensis*, Lind., is visited and fertilised in Natal by honey-suckers and by small bees (233).

## ORD. ACANTHACEÆ.

*Thunbergia alata*, Boj.—The insect entering the tube of the flower to reach the honey at the base first touches the stigma with its back, and then the anthers, which are provided inferiorly with pointed processes (352).

*Cryphiacanthus barbadensis*, Nees. (*Ruellia clandestina*, L.).—The cleistogamic flowers were known to Dillenius (531).

*Eranthemum*, L., *Dædalacanthus*, Anders., *Dipteracanthus*, Nees,<sup>1</sup> *Æchmanthra*, Nees., and *Ruellia*, L., also possess cleistogamic flowers (167).

*Meyenia erecta*, Benth.—The mechanism of the flower of this West African shrub has been described by Mr. Irwin Lynch (444). The flowers stand nearly horizontal. The style lies in a groove on the dorsal side of the tubular curved corolla. The stigma, which stands at the mouth of the tube, is two-lipped; its upper lip, which is alone receptive, is rolled into a tube.

The anthers stand midway in the corolla tube, and are furnished with hairs which catch the pollen as it is being shed. The broad lower lip of the stigma projects downwards, obstructing the entrance; it first acts as a lever to bring the upper lip down upon the back of an insect entering the flower; but afterwards, as the insect emerges with its back dusted with fresh pollen, the lower lip of the stigma protects the upper one from contact.

*Strobilanthes* (*Goldfussia*) *anisophylla*, Nees.—This flower was carefully described and beautifully figured by Charles Morren in 1839 (541A). Morren saw that insects were needed to effect fertilisation, but he thought only of self-fertilisation, and accordingly he misinterpreted the mechanism of the flower.

The flowers stand nearly horizontal. The tip of the style only bears stigmatic papillæ on its lower (anterior) surface; it is curved upwards so that an insect in entering the flower comes at once in contact with the stigma. When the stigma is touched (or even if it be breathed upon) it at once becomes straightened out and generally curves at the same time to the right, and it becomes closely appressed to the inferior wall of the corolla. The insect passes further into the flower, and becomes dusted with fresh pollen: this is carried out of the flower without coming in contact with the stigma. According to Morren the irritability of the style is never manifested until after dehiscence of the anthers.

<sup>1</sup> Bentham and Hooker place this genus under *Ruellia*.

Morren supposed that the pollen fell of itself from the anthers, and either came directly, or was carried by small insects, to the hairs upon the inferior wall of the corolla in the neighbourhood of the stigma; and that thus, when by any cause the style was irritated, the stigma curved over and applied itself to the pollen.

*Acanthus mollis*, L., and *A. spinosus*, L.—The four unilocular anthers lie close together and hold between them the loose pollen. The inferior filaments pass below and in front of the anthers, and are suddenly bent back towards them immediately below their attachment. The bee-visitors (*Bombus italicus* and *B. terrestris*) have to pass between these inferior filaments, and in doing so force both them and their anthers apart, and cause the pollen to fall out. The proterandrous condition lasts for several days, and then the end of the style, which was straight before, bends downwards and forwards, so that the lobes of the stigma come in contact with the bee (172, 178, 360).

*Aphelandra pectinata*, Willd. (*A. cristata*, H. B. and Kth).—The two lobes of the corolla which form the upper lip are rolled round the anthers; the two lateral lobes are approximated, forming folding doors which close the entrance of the tube. When these doors are opened they cause the lobes of the upper lip also to separate, and the anthers are set free and shed their pollen on the visitor. The fertilising-agents are probably humming-birds (178).

*Rhinacanthus communis*, Nees., is markedly proterandrous. In the first stage, the two anthers are bent down into the entrance of the flower, and the still immature stigma is bent upwards; in the second stage the anthers are bent apart to the sides, and the ripe stigma is placed exactly in the path of the insect's proboscis. The visitors are probably Lepidoptera (177).

#### ORD. SELAGINEÆ (GLOBULARIACEÆ).

*Globularia vulgaris*, L., is proterandrous; *G. cordifolia*, L., and *G. nudicaulis*, L., are protogynous with persistent stigmas. The flowers of all three are light-blue and adapted for fertilisation by butterflies. This is the only instance in the German and Swiss flora of a blue colour being produced by the selective agency of Lepidoptera (609).

## ORD. VERBENACEÆ.

*Ægiphila elata*, Sw., and *Æ. mollis*, H. B. and Kth., are conspicuously heterostyled. *Æ. obdurata* "probably was once heterostyled, and has since been rendered diœcious by the pistil in the one form and the stamens in the other having become functionless and reduced in size" (Darwin, 167, p. 124).

*Verbena officinalis*, L., is adapted for fertilisation by bees (590, III., and 609).

The flowers of a *Lantana* in South Brazil are, according to Fritz Müller, yellow on the first day, orange on the second, and purple on the third. Some butterflies visit the yellow and orange flowers, some exclusively the yellow, *none* the purple. So this change of colour increases the conspicuousness of the plant, and at the same time saves many useless visits (560).

*Ocimum*, L.—In this genus the Labiate type of flower is reversed, the stamens and style lying upon the under lip, while the upper side of the tube lodges the honey, which is protected by hairs on the superior stamens. Therefore the stamens first curve upwards, the style downwards, and afterwards in the contrary direction; which is the reverse of what occurs in *Teucrium*, for instance. The fertilisers are bees of the genera *Anthidium*, *Apis*, *Bombus*, and *Halictus* (178, 360).

## ORD. LABIATÆ.

*Plectranthus fruticosus*, L'Hér.—The reproductive organs lie below the entrance into the honey-receptacle, which is a spur-like development of the base of the corolla. In the first stage the style lies with unripe stigmas between the stamens; in the second the stamens have spread apart, and the style with outspread stigmas stands alone in the way of insect-visitors (360).

336. *LAVANDULA VERA* (L.), D. C.—The spikes of small blue flowers attract many insects, especially bees, by their strong scent, and supply abundant honey. The tube is 6 mm. long, and the nectary resembles that of *Thymus* in size and position. The stamens, which lie in the inferior side of the tube, overtop the stigmas, but the well-marked proterandry insures cross-fertilisation.

(1) *Anthophora quadrimaculata*, Pz. ♀ ♂, ab.; (2) *Osmia aenea*, L. ♂, freq.; (3) *O. rufa*, L. ♀, s.; (4) *Megachile pyrina*, Lep. (*fasciata*, Sm.), ♂,

freq. ; (5) *M. Willughbiella*, K. ♂ ; (6) *M. centuncularis*, L. ♂ ; (7) *Anthidium manicatum*, L. ♀ ♂, ab. ; (8) *Crocisa scutellaris*, Pz. ♀ ♂, ab. ; (9) *Cœlixys conoidea*, Ill. ♀, freq. ; (10) *C. umbrina*, Sm. ♀ ; (11) *Chelostoma nigricorne*, Nyl. ♂, all only sucking. See also No. 590, III.

337. *MENTHA ARVENSIS*, L.—The base of the ovary, which secretes the honey, is several times as large as the ovary itself, (*n*, 4, Fig. 159). The corolla forms a bell, which in the pistillate flowers is about 2 mm., in the hermaphrodite about 3 mm. long, and in both is fully half as wide at the mouth as it is long. The honey is accessible to very short-lipped insects, and it is completely sheltered from rain by hairs which extend from the sides of the bell to its centre. The flowers make themselves perceptible at a

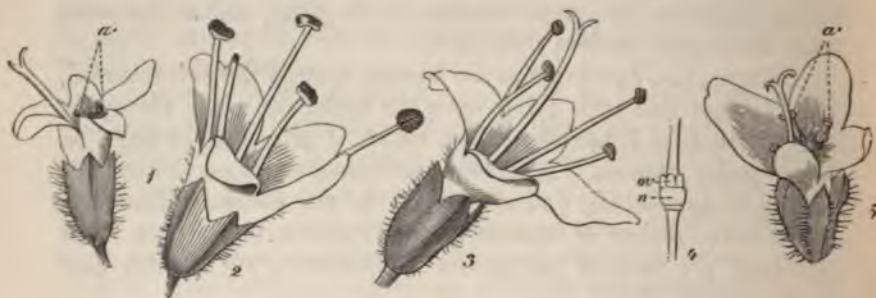


FIG. 159.

1-4.—*Mentha arvensis*.

1.—Female flower.

2.—Hermaphrodite flower. In first (male) stage.

3.—Ditto, in second (female) stage.

4.—Ovary and nectary.

5.—*M. aquatica*. Female flower, seen obliquely from the front, to show the rudimentary stamens.

Figs. 1 and 5 should be horizontal.

distance by their scent, and their close whorled arrangement renders them conspicuous to the eye, still more in the case of the large-flowered hermaphrodite than the smaller female plants. I have verified by direct observation in the case of *Mentha* the opinion to which I shall recur in describing *Nepeta* and *Thymus*, that insects visit the more conspicuous flowers before those that are less so ; in the case of *Nepeta* and *Thymus* I have neglected to study this point sufficiently.

Visitors : A. Diptera—(a) *Stratiomyidæ* : (1) *Odontomyia viridula*, F. ; (b) *Syrphidæ* : (2) *Eristalis sepulcralis*, L., very ab. ; (3) *Syritta pipiens*, L., ab. ; (4) *Melithreptus scriptus*, L. ; (5) *M. tæniatus*, Mgn., both not rare, s. ; (c) *Muscidæ* : (6) *Onesia floralis*, R. D. ; (7) *O. sepulcralis*, Mgn., both ab. ; (8) *Lucilia silvarum*, Mgn. ; (9) *L. cornicina*, F. ; (10) *Pyrellia cadaverina*, L. ;

(11) *L. albiceps*, Mgn., the last four species not rare. B. Lepidoptera—*Rhopalocera*: (12) *Satyrus Janira*, L. All these insects sucked honey only, though I expected to see the Syrphidæ at least eating pollen.

338. *MENTHA AQUATICA*, L. (*M. hirsuta*, Sm.).—While in *Mentha arvensis* small-flowered female and large-flowered hermaphrodite flowers occur in nearly equal numbers, in *M. aquatica* the former are much rarer than the latter. In the hermaphrodite flowers the tube is 4 to 5 mm. long, and about 2 mm. wide at the mouth; otherwise the flower resembles that of *M. arvensis*. Although, owing to the greater length of the tube, the honey is slightly less accessible than in *M. arvensis*, insect-visits are more numerous, owing to the taller stalks and the larger, denser heads of flowers.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Halictus cylindricus*, F. ♂; (2) *H. maculatus*, Sm. ♂, both ab.; (3) *H. longulus*, Sm. ♂; (4) *H. nitidiusculus*, K. ♂, all s.; (b) *Ichneumonidæ*: (5) Various sp., some creeping bodily into the flowers. B. Diptera—(a) *Empidæ*: (6) *Empis rustica*, Fallen; (7) *E. livida*, L., both ab., s.; (8) *E. tessellata*, F., do.; (b) *Syrphidæ*: (9) *Ascia podagrica*, F., s.; (10) *Eristalis nemorum*, L.; (11) *E. arbustorum*, L.; (12) *E. æneus*, Scop.; (13) *E. sepulcralis*, L., all four very ab., sometimes s., sometimes f.p.; (14) *Syritta pipiens*, L., ab.; (15) *Helophilus pendulus*, L., ab.; (16) *H. trivittatus*, F.; (17) *Syrphus pyrastris*, L., ab.; (18) *Melanostoma mellina*, L., ab., these also both s. and f.p.; (c) *Muscidæ*: (19) *Onesia floralis*, R. D.; (20) *O. sepulcralis*, Mgn.; (21) *Sarcophaga carnaria*, L.; (22) *Musca corvina*, F., all four very ab.; (d) *Tabanidæ*: (23) *Chrysops cæcutiens*, L., s.

Delpino considers *Mentha* and *Coleus*, Lour., degraded forms of the Labiate type (No. 178, p. 143; 360, p. 656); he, however, gives no reason for thinking them to be such, and not rather less specialised forms, differing less from the common ancestors of the Labiates.

The flower of *Coleus (Blumei)*, Benth. (?) is figured and described in No. 560, III.

339. *LYCOPUS EUROPEUS*, L.—The corolla forms a bell 3 to 4 mm. long, 2½ mm. wide at the mouth, but scarcely 1 mm. wide at the base. Honey is secreted by the yellow fleshy base of the ovary; it is accessible to very short-lipped insects, and is sheltered from rain by long hairs which project from the sides of the bell towards its centre. Some purple spots on the under lip serve as guides.

The flowers are markedly proterandrous. When the two anthers which project from the tube come to maturity, the two stigmas still lie folded together (Fig. 160, 1). When the stigmas

to the small size of the flower; and that the small size of the flower causes every with them. The same explanation holds



FIG. 160.—*Lycopus europaei*

- 1.—Flower, in first (male) stage, from below.
  - 2.—Ditto, in second (female) stage, from the side. This.
  - 3.—Ditto, in first stage, after removal of the under lip, from below.
- a, abortive stamens; n, nectary; a', perfect anthers, b, stigma; a<sup>2</sup>, ditto, withered; st', stigma, still immature; st<sup>2</sup>, ditto, ripe.

flowers are the smallest among Scrophulariaceae among Labiates.

Visitors: A. Hymenoptera—*Vespidæ*: (1) *diadema*, s., freq. (Thur.). B. Diptera—(a) *scriptus*, L., s. and f.p.; (3) *Syritta pipiens*, L. *scidæ*: (4) *Lucilia silvarum*, Mgn.; (5) *L. c.* *Sarcophaga albicans* Mon. ab. s.; (7) *Pollenia*

hermaphrodite ones; his theory rests, if I understand it rightly, upon the two following arguments. Since no stigmas are mature at the time when in the first flowers of a proterandrous plant the stamens dehisce, these stamens are of no use to the plant, and since all economy of useless organs is advantageous to the plant, the stamens of the first flowers of proterandrous plants can be abolished by Natural Selection. This reasoning is undeniably correct, but it applies only to the first flowers of proterandrous plants, and not to

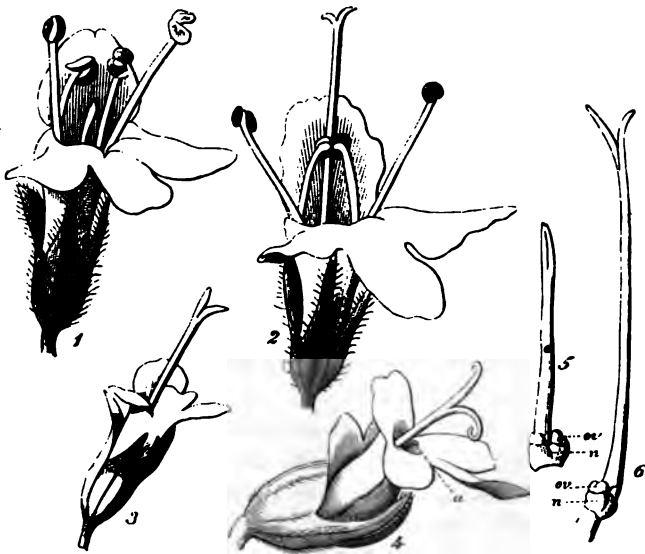


FIG. 161.

1—3.—*Thymus Serpyllum*, Fr.

1.—Hermaphrodite flower, in first (male) stage.

2.—Ditto, in second (female) stage.

3.—Female flower.

4—5.—*T. vulgaris*, L.

4.—Female flower.

5.—Pistil of hermaphrodite flower in first stage.

6.—Ditto, in second stage. ov, ovary; n, nectary. (× 7.)

the female stocks of *Thymus* which bloom all summer beside the hermaphrodite ones. This in my opinion is only to be explained in the way that I have suggested in the case of *Nepeta* (p. 484). The variability in size, which my theory presupposes, is present in our two species of *Thymus*, as in *Nepeta*, to such a degree that, while the largest hermaphrodite flowers (Fig. 161, 1, 2) are several times as large as the smallest female (Fig. 161, 3), the smallest hermaphrodite and the largest female flowers are nearly equal in size. The flowers

on the same stock, on the contrary, are all much of the same size, as my explanation requires, but the hermaphrodite flowers enlarge in passing from the first (male) to the second (female) stage. The certainty of cross-fertilisation, which is also necessary for my theory, is in a high degree a character of *Thymus*; for the honey is exceedingly abundant and has an aromatic taste, the base of the ovary by which the honey is secreted ( $n$ , 5, 6) is many times as large as the ovary itself, the aggregation of the flowers and their strong scent reveal them to insects and permit insects to visit many with little loss of time, and from the reproductive organs protruding beyond the corolla many flowers may be fertilised at once as the insect clammers over the inflorescence. The tube is smooth at the base where the honey lies, and lined with hairs above to exclude rain; it is only a few millimetres long ( $2\frac{1}{4}$  to 4 mm. in *T. Serpyllum*), so that the honey is accessible to a great variety of insects. Self-fertilisation was impossible in all the flowers that I have examined, for the style, which in the first stage is short and overtopped by the anthers (Fig. 161, 1, 5), elongates and grows out beyond the anthers before its two divisions with the stigmatic papillæ at their tips spread apart.<sup>1</sup>

Darwin found the female form very much more productive than the hermaphrodite, both in *T. Serpyllum* and *T. vulgaris*.

While Darwin in England, Hildebrand in the Rhine Provinces, Ascherson, according to his *Flora*, in Brandenburg, and I in Westphalia and Thuringia, have only observed the two forms, female and hermaphrodite, of this plant, Delpino, near Florence, has found the plant trimorphic: he states that it consists there of hermaphrodites with both stamens and pistil equally developed; of others with greatly developed stamens and the pistil in every stage of abortion, or even absent; and finally, others with greatly developed pistil and more or less aborted stamens (No. 173, p. 7). In England also there seems to be a passage towards purely male flowers, for, according to Dr. Ogle (No. 632, p. 54), in many of the hermaphrodite flowers the stigma never reaches maturity. Without accurate information concerning the size of the flowers, the time of their development, the frequency of insect-visits, and the relative distribution of the two forms, all attempts at explanation must be unsatisfactory.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, s. and c.p., ab.; (2) *Bombus pratorum*, L. ♀, do.; (3) *Saropoda bimaculata*, Pz. ♀ ♂.

<sup>1</sup> Compare my account of *Nepeta Glechoma*, p. 484, and Darwin's account of *Thymus*, No. 167, p. 300.

ab. ; (4) *Andrena nigroænea*, K. ♀, s. ; (5) *Megachile circumcincta*, K. ♂, s. ; (6) *Nomada germanica*, Pz. ♀, s. ; (7) *Cœlixys* sp. ♂, s. ; (b) *Sphegidae* : (8) *Ammophila sabulosa*, L. ♀ ♂, s., ab. ; (9) *Cerceris variabilis*, Schr. ♀ ♂, s. ; (10) *Lindeniæ albilabris*, F., s. B. Diptera—(a) *Bombylidae* : (11) *Systoechus sulfureus*, Mik., s. ; (b) *Syrphidae* : (12) *Eristalis arbustorum*, L., very ab., s. ; (13) *E. sepulcralis*, L., s. ; (14) *Syritta pipiens*, L., s., ab. ; (15) *Volucella bombylans*, L., s. ; (c) *Conopidae* : (16) *Conops flavipes*, L., s. ; (17) *Sicus ferrugineus*, L., s. ; (18) *Myopa testacea*, L., s. ; (d) *Muscidae* : (19) *Lucilia cornicina*, F. ; (20) *Echinomyia tessellata*, F. ; (21) *Gymnosoma rotundata*, L. ; (22) *Ocyptera brassicaria*, F., ab. ; (23) *Sarcophaga carnaria*, L., very ab. ; (24) *S. albiceps*, Mgn., very ab., all only sucking. C. Lepidoptera—(a) *Rhopalocera* : (25) *Satyrus pamphilus*, L. ; (26) *S. Janira*, L. ; (27) *Argynnis Aglaia*, L. ; (28) *Lycæna icarus*, Rott. ; (b) *Sphinges* : (29) *Sesia empiformis*, Esp (Almethal) ; (30) *S. tipuliformis*, L.,—all sucking. See also No. 590, III., and No. 609.

I have observed altogether on *T. Serpyllum*.—

	Apidæ.	Lepidoptera.	Diptera.	Other Insects.	Total.
In the Lowlands ..	17	20	30	5	72
In the Alps ... ..	25	65	30	2	122

In every 100 insect-visitors there are, therefore :—

	Apidæ.	Lepidoptera.	Diptera.	Other Insects.	Total.
In the Lowlands ...	23·6	27·7	41·6	6·9	99·9
In the Alps ... ..	20·5	53·2	24·6	1·6	99·9

341. *THYMUS VULGARIS*, L.—I have observed the following visitors in my garden :—

A. Hymenoptera—(a) *Apidæ* : (1) *Apis mellifica*, L. ♀, s. ; (2) *Halictus*, small species, s. and c.p. ; (b) *Sphegidae* : (3) *Ammophila sabulosa*, L. ♀ ♂, s. B. Diptera—(a) *Empidae* : (4) *Empis livida*, L., s. ; (b) *Syrphidae* : (5) *Syritta pipiens*, L., s. and f.p., ab. ; (c) *Muscidae* : (6) *Sarcophaga albiceps*, Mgn., s., ab. C. Lepidoptera—*Sphinges* : (7) *Sesia tipuliformis*, L., s.

342. *ORIGANUM VULGARE*, L.—This plant agrees with *Thymus* in consisting of large-flowered proterandrous hermaphrodite, and small-flowered female individuals, and in the whole mechanism of the flowers ; and if it is inferior to *Thymus* in perfume and in the

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, freq.; (3) *Halictus cyllini* F. ♂, both species very ab.; (5) *H. nitidus*, F. ♂, both species very ab.; (6) *Empis livida*, L.; (7) *Empis*, s.; (8) *Ascia podagrica*, F. storum, L., s. and f.p., ab.; (10) *E. nemorum*, dulus, L., s.; (c) *Conopidae*: (12) *Sicus ferrugineus* Rondani; (14) *M. variegata*, Mgn., all three *Ocyptera brassicaria*, F.; (16) *O. cylindrica*, F. siberita, F., ab., all three s. C. Lepidoptera: *Janira*, L., s.; (19) *S. hyperanthus*, L., s. No. 609.

*Satureia hortensis*, L., is gynodioecious and is much more productive than the heterostylous form (No. 590, III.).

343. *CALAMINTHA CLINOPODIUM*, Sp. The nectaries and honey-receptacle are Labiate type. The corolla-tube is 10 to 12 mm. long, filled for a space of 3 mm. with honey.

The inferior division of the style forms a broad lamina, which is bent downwards and bears two papillæ; the upper is much narrower and of varying size. There is still more staminal development of the stamens, some or all of which are completely aborted in many flowers. This shows us how Natural Selection could

344. *CALAMINTHA ACINOS*, L. :—

Visitors : A. Hymenoptera—*Apidæ* : (1) *Apis mellifica*, L. ♀, s. and c.p., ab. (Thur.). B. Diptera—*Bombylidæ* : (2) *Systæchus sulfureus*, Mik., s. (Thur.).

*Calamintha alpina*, Lam.—Both large-flowered and small-flowered plants occur, the flowers of both being hermaphrodite and proterandrous, but only the small flowers being capable of spontaneous self-fertilisation.

The plant is visited by Syrphidæ and by a great number of bees and Lepidoptera (584, 609).

*Horminum pyrenaicum*, L.—The dark-blue colour, the odour, and the very abundant honey attract numerous insects, while the marked proterandry renders self-fertilisation impossible (No. 609, fig. 125).

345. *MONARDA DIDYMA*, L.—I have seen this plant visited by *Plusia gamma*, L.

*Monarda ciliata* (?) is adapted for fertilisation by Sphingidæ (228).

*Rosmarinus*, L., according to Delpino, is proterandrous, and the stigma comes to take the place of the anthers (178).

346. *SALVIA PRÆTENSIS*, L.—The remarkable mechanism of this flower, and the way in which it is fertilised by humble-bees, was so thoroughly explained and figured by Sprengel<sup>1</sup> that Hildebrand, in his work on *Salvia* (345), has described nothing new, except the proterandrous condition, which Sprengel had overlooked.

Honey is secreted by the yellow, fleshy base of the ovary. The corolla is horizontal; the under lip forms a convenient platform for insects, and the erect, helmet-shaped upper lip incloses the anthers. In the first stage, the style, with its stigmatic branches still folded together, protrudes almost horizontally from the upper lip, in the second it points downwards with divergent and recurved stigmas. The entrance to the tube is guarded by two lamellæ which converge and coalesce with one another anteriorly; these lamellæ are attached to the inferior limbs of the enormously long connectives of the two stamens, and are produced by metamorphosis of the inferior anther-lobes; the other and much longer limb of each of the two connectives rises up under cover of

<sup>1</sup> 702, pl. 1. figs. 18, 24-33, 39, 42.

draws its head, the connectives with the former position. In old flowers the bee t

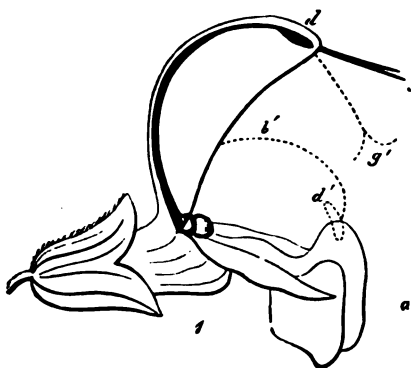


FIG. 162.—*Salvia pratensis*,

- 1.—Flower, from the right side.
  - 2.—Stamens, seen obliquely ( $\times 2$ ).
- a, filament; b, upper arm of the connective; c, lower arm  
c, inferior ditto, transformed into a lamina closing up the tu  
inferior anther-lobes; g, style in first stage; g', style in second  
the position of the anthers when rotated forwards.

sides of the recurved branches of the now  
The superior pair of anthers in this and  
of *Salvia* is present in the form of

described above, and effect cross-fertilisation regularly, I have only noted the following:—

(1) *Bombus silvarum*, L. ♀ and ♂; (2) *Osmia rufa*, L. ♀; (3) *Anthidium manicatum*, L. ♀ (very freq.); (4) *Megachile pyrina*, Lep. (*fasciata*, Sm.), ♂, all sucking normally.

Among useless visitors Sprengel mentions (p. 61) cabbage-white butterflies, which insert their proboscis in the small space between the lower anther-lobes and the corolla, and obtain the honey without effecting fertilisation. I have seen *Plusia gamma*, L., acting in the same way, I have also seen small bees in abundance (*Prosopis communis*, Nyl. ♂ ♀, *Halictus sexstriatus*, Schck. ♀, *H. nitidus*, Schck. ♀, *H. nitidusculus*, K. ♀, *H. morio*, F. ♀) creeping into the flowers and reaching the honey without causing more than a slight and ineffectual movement of the levers. The position of the anthers quite prevents flies from stealing the pollen of this flower, and I have never observed a bee sweeping the anthers with its tarsal brushes. Delpino (No. 567, pp. 9, 10) unjustly questions my statement "that in *Salvia* the anthers are more or less protected from insects, which are restricted mainly or exclusively to the honey." A further list of visitors in Low Germany (twelve Apidæ, two Bombylidæ) is given in No. 590, III. On the Alps I have seen the flowers visited by the hive-bee, by six humble-bees, eleven Lepidoptera, and Rhingia (609).

This species is gynodioecious. In addition to the large-flowered hermaphrodite plants, small-flowered female plants occur, in whose flowers the now functionless lever-apparatus shows all degrees of abortion.

This species is remarkable above all other cases of gynodioecism, because it shows us the gradual abortion of all the stamens of a flower in four distinct stages: (1) The first of the five stamens, which must have been placed in the median line of the corolla superiorly, and is still present, more or less altered, in many Scrophularinæ (*Scrophularia*, *Pentstemon*), had already disappeared in the common ancestors of the Labiates. (2) The two upper stamens of the remaining four were reduced to tiny stalked knobs in the ancestors of the genus *Salvia*. (3) The inferior anther-lobes of the two remaining stamens produce pollen to a greater or less extent in *S. officinalis*, *S. porphyrantha*, and *S. triangularis*, but in *S. pratensis* they are transformed into two hollow laminæ which coalesce anteriorly. (4) In the small-flowered female form of *S. pratensis*, the superior anther-lobes also have become useless, and subject to degeneration in common with the whole of the lever-apparatus (570, vol. xvi.; 609).

*Salvia Sclarea*, L., *S. æthiopica*, *S. argentea*, L., *S. virgata*, Ait., *S. pendula*, Vahl., and *S. rubra*, Spr., have the same mechanism according to Hildebrand as *S. pratensis*. In *S. nutans*, L. (Hild. figs. 4-7), on the other hand, the rotation of the connectives

adheres readily to them. As the anthers dehisce more widely and permit the pollen to escape, the style elongates and extends beyond the shorter anthers, often bringing the stigmas in contact with the pollen; finally it protrudes far beyond the anthers, and in this position is always touched before the anthers by an insect-visitor; probably the pollen brought from another flower and thus



FIG. 164.—*Stachys Betonica*, Benth.

- 1.—Flower, in first (male) stage, from the side ( $\times 2\frac{1}{2}$ ).
- 2.—Forepart of ditto ( $\times 7$ ).
- 3.—Flower in second (female) stage ( $\times 2\frac{1}{2}$ ).
- 4.—Forepart of ditto ( $\times 7$ ).
- 5.—Ovary and nectary ( $\times 7$ ).

applied outstrips in its action that which is so often applied in the previous stage when the stigma is making its way past the anthers.

A. Hymenoptera—*Apidae*: (1) *Bombus agrorum*, F. ♂ ♀ (10—15), ab., s. B. Diptera—*Syrphidae*: (2) *Volucella bombylans*, L. (7—8), c.p. (Sld.); (3) *Eristalis horticola*, Mgn. (Sld.), c.p. C. Lepidoptera—*Sphingidae*: (4) *Zygaena lonicerae*, Esp., s., freq. (Thur. July 12, 1868). Additional visitors (five bees and four Lepidoptera) are enumerated in No. 590, III.

*Sideritis romana*, L.—The reproductive organs are inclosed within the tubular flower; the style is very short; the longer stamens are of the usual form; each of the shorter stamens bears a semicircular connective which has at one end a perfect, and at the other a rudimentary, anther-lobe. The two connectives form together a complete circle, through which an insect must thrust its

of the inferior, and the two connectives lie so close together that one moves with the other. A bee in entering first thrusts its head against the two inferior anther-lobes, and thus causing the connectives to rotate, it is immediately afterwards struck on the back by the two superior anther-lobes. The pollen thus placed on the bee's head and back is rubbed off in older flowers upon the two stigmas, which are divergent and much bent downwards.

Dr. Ogle gives a very detailed description of this species of *Salvia* (631), and rightly lays stress upon the following additional points as special adaptations: (1) the convexity of the upper lip, which causes the growing style to take such a direction that afterwards its outspread stigmas must come in contact with the bee's back; (2) the bulging of the upper wall of the anterior part of the tube, which gives the inferior anther-lobes free play when the connectives rotate; (3) the shortness and stiffness of the filaments, which give a steady fulcrum for the connectives; (4) the divergence of the filaments, which leaves a free entrance for the bee.

Besides the hive-bee, which Sprengel and Hildebrand also saw, I have observed *Bombus silvarum*, L. ♀, *Anthophora æstivalis*, Pz. ♀, *Anthidium manicatum*, L. ♀, *Osmia rufa*, L. ♀, as regular fertilisers; all were sucking honey exclusively. Of useless guests, Hildebrand observed a butterfly, which could easily reach the honey with its proboscis without dusting itself with pollen. I have seen a small species of bee with abdominal collecting-brushes, *Chelostoma campanularum*, ♀ ♂, repeatedly creeping in and out of the flowers without being dusted with pollen; and Herr Borgstette sent me, from Teklenburg, *Prosopis communis*, Nyl. ♀, which he had caught on the flowers. A further list of visitors is given in No. 590, III.

According to Delpino, the anthers of *S. officinalis*, like those of *Sideritis*, are provided with sticky glands (178).

*Salvia porphyrantha* resembles *S. officinalis* in the arrangement of its connectives, and in the inferior anther-lobes being filled with pollen, though with a smaller quantity than that present in the superior lobes.<sup>1</sup>

*Salvia glutinosa*, L., according to Dr. Ogle (631), differs from *S. officinalis* in that the inferior anther-lobes are quite barren and are withdrawn within the tube, and that the inferior, not the superior, side of the anterior part of the tube bulges out. It is fertilised by large humble-bees; small humble-bees, and hive-bees whose proboscis is too short to reach the honey legitimately,

<sup>1</sup> According to Mr. T. H. Corry.

bite a hole in the superior side of the tube immediately over the nectary and steal the honey. Dr. Ogle found 90 per cent. of the flowers bitten through, and I have always found the flowers bitten through and robbed of their honey by an Alpine robber-bee, *Bombus mastrucatus*, Gerst. ♂ (609).

*Salvia nilotica*, Vahl. (345, figs. 24, 25).—The main point in which the flowers differ from those of *S. officinalis* is that the two inferior anther-lobes lie freely side by side, and the connectives can be caused to revolve separately. Hildebrand saw them visited by bees.

*S. verticillata*, L. (345, figs. 26-30; 172), has immovable connectives, but an upper lip which folds back when touched by an insect-visitor, and exposes the two superior anther-lobes to contact with it. The style, which would hinder this movement if in its usual place, is lower down. Hildebrand saw this species also visited by bees. According to Delpino, the anthers, like those of *Sideritis* and of *S. officinalis*, are provided with sticky glands (178, p. 145). *S. verticillata* is visited by numerous species of bees and humble-bees (590, III.; 609).

In *S. patens*, Cov. (172, 345, fig. 31), the anthers project partly or entirely beyond the upper lip. The connectives are versatile, and the lower anther-lobes are metamorphosed into lamellæ; the style is so fixed between the upper arms of the connectives that when the connectives revolve it is carried forwards and downwards with them, and its stigma, which projects beyond the anthers, is thus brought first in contact with the insect's back. Ogle's account (631) agrees with Hildebrand's. But while Hildebrand considers self-fertilisation and cross-fertilisation as alike possible, Ogle shows that cross-fertilisation is insured. When an insect-visitor strikes the lower arm of the connective, its back is touched by the anthers and a little farther back by the stigma, and the space between the two points is increased by the lower stigma being very short in comparison with the upper. As the insect passes further in, anthers and stigma rub along its back, but no pollen from the anthers reaches the stigma of the same flower. As the insect draws back anthers and stigma return to their places below the upper lip; in the next flower the stigma comes in contact with a part of its back already dusted with pollen. In several flowers Dr. Ogle found the style shorter than the anthers; in such flowers insects might lead to self-fertilisation as well as cross-fertilisation. Ogle states the very surprising fact that the honey in *S. patens* is not secreted by the base of the ovary as is usually

the case in Labiates, but by a thick tuft of glandular hairs on the corolla, immediately above a constriction which completely shuts off the lower part of the tube that usually serves as a honey-receptacle.

In *S. austriaca*, Jacq. (345, figs. 32-35), the anther-lobes stand far apart and project beyond the upper lip. If the lower arms of the two connectives are thrust inwards the upper arms converge, and the anther-lobes (moving downwards and forwards) strike against each other in front of the mouth of the flower.

*S. triangularis*, Thunb. (345, figs. 36-39), has immovable connectives, almost straight, and lying parallel to the long axis of the flower; they have a fully-formed anther-lobe at each end. The two anterior anther-lobes project from the mouth of the flower, and are the first to touch the insect's back; the two posterior, which stand in the entrance, touch its sides immediately afterwards. In the second stage the stigma stands in front of the anterior anther-lobes, and is touched first of all by the insect.

*S. tubiflora*, Sm. (345, figs. 40, 41).—The mechanism of this flower resembles that of the last-named species in all important points, except that the inferior arm of each connective bears, instead of an anther-lobe, an elongated lamina which lies in contact with the upper lip.

348. *SALVIA SILVESTRIS*, L., agrees on the whole in its floral mechanism and in its proterandrous condition with *S. pratensis*, but its flowers are so much smaller that a proboscis only 4 mm. long suffices to reach the honey. I observed as its natural fertilisers in Thuringia: (1) *Apis mellifica*, L. ♀ (6), sucking honey, and dusting the top of its head with pollen and afterwards applying it to the stigma in older flowers; (2) a wasp, *Psammophila affinis*, K. ♀ (4), in abundance, sucking honey; and as useless visitors, (3) *Pieris rapæ*, and (4) *P. napi*.

*Salvia cleistogama*, de Bary and Paul, when transplanted to Halle from Africa, bore only cleistogamic flowers for five years (Ascherson, 10). Ascherson considered that the plant afforded an example of continuous self-fertilisation; but he himself afterwards observed ordinary open flowers (11).

Scarlet species of *Salvia* in South Brazil are visited very abundantly by humming-birds (Fritz Müller, No. 359); so likewise are species of *Salvia* in the Cordilleras (Darwin, No. 164, p. 371).

*Salvia splendens*, Sellow (distinct from the plant described under this name by Hildebrand).—According to Mr. W. Trelease

this plant is very abundantly visited by humming-birds, and is adapted for them in the following characters: the small under lip, scarcely fit for a standing-place, the very large amount of honey, and the bright scarlet colour of the calyx and corolla (735).

349. *NEPETA GLECHOMA*, Benth. (*Glechoma hederacea*, L.).—In the small-flowered female form, the tube is  $6\frac{1}{2}$  to 8 mm. long, widening in the anterior half to a diameter of only  $1\frac{1}{2}$  to  $2\frac{1}{2}$  mm. laterally, and rather less antero-posteriorly: in the large-flowered hermaphrodite plants the tube is 9 to 16, usually 14 to 16 mm. long, and, for the greater part of the anterior half,  $2\frac{1}{2}$  to  $4\frac{1}{2}$  mm. broad, being slightly less in the antero-posterior diameter. The honey in the small female flowers is accessible to all our humble-bees, while the large, hermaphrodite flowers, by widening anteriorly to admit the bee's head, render their honey accessible to all except *B. terrestris*, L.

The existence of plants bearing only small female flowers in *Nepeta* and also in *Origanum*, *Thymus*, *Mentha*, and others, is not to be explained merely by the necessity of insuring cross-fertilisation; for in all these genera cross-fertilisation is completely provided for by the hermaphrodite forms alone. But the following view of the small-flowered female plants is intelligible:—

Of the flowers of the same species growing together, the most conspicuous are first visited by insects, and if the flowers on some plants are smaller than on others, perhaps owing to scanty nourishment, they will generally be visited last. If the plant is so much visited by insects that cross-fertilisation is fully insured by means of proterandrous dichogamy, and self-fertilisation is thus rendered quite needless, then the stamens of the last-visited small-flowered plants are useless, and Natural Selection will tend to make them disappear because the loss of useless organs is manifestly advantageous for every organism.

This explanation rests upon the hypotheses, (1) that the flowers of those species in which small-flowered female plants occur together with large-flowered hermaphrodite plants are plentifully visited by insects and are markedly proterandrous; (2) that variation in size of the flowers has always taken place, not among the flowers on a single plant, but between the flowers on different individuals.

Both hypotheses are well founded. For (1) the flowers of *Nepeta*, *Thymus*, *Origanum*, and *Mentha* are plentifully visited by insects and are markedly proterandrous, while proterandry has

been quite wrongly ascribed to many other Labiates. The styles in these four genera are still applied closely together after the anthers have dehisced, and though when the styles separate the anthers may be still coated with pollen, self-fertilisation is prevented by the style projecting far beyond the anthers. In species where cross-fertilisation is less perfectly insured, and which produce seed frequently by self-fertilisation, the smaller hermaphrodite flowers can never become transformed into purely female flowers, since their anthers are always of real service, and cannot be removed by natural selection. And (2) it cannot be doubted that, in *Nepeta*, *Thymus*, *Origanum*, and *Mentha*, the size of the flowers has been subject to great variations, since the same condition occurs even now, at least in *Nepeta* and *Thymus*. While flowers of the same age on a single plant differ little in size, we find on different plants all intermediate grades in size, between the smallest female and the largest hermaphrodite flowers; and the largest female flowers are quite as large as the smallest hermaphrodite.

Darwin<sup>1</sup> adduces several weighty objections to this view, and my own observations on *Centaurea Jacea* also militate against it. Darwin prefers to ascribe the gynodioecious condition to increased fertility. He supposes that either some individuals tended to produce more seed, and consequently less and less pollen, until finally their stamens disappeared; or else that the stamens of certain individuals began to show a tendency to abort, and that these individuals consequently produced more seed.

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus agrorum*, F. ♂ ♀ (10—15); (2) *B. confusus*, Schenck, ♀ (12—14); (3) *B. lapidarius*, L. ♂ (10—12); (4) *B. hortorum*, L. ♂ ♀ (18—21); (5) *B. pratorum*, L. ♀ (11—12); (6) *B. Rajellus*, Ill. ♀ (12—13); (7) *B. silvarum*, L. ♀ (12—14); (8) *B. (Apathus) Barbutellus*, K. ♀ (12); (9) *B. (A.) vestalis*, Fourc. ♀ (12); (10) *B. (A.) rupestris*, F. ♀ (11—14); most of these species very ab., sucking both female and hermaphrodite flowers in the normal way; (11) *B. terrestris*, L. ♀ (7—9), always bores through the corolla of the hermaphrodite flowers, and sometimes of the small female flowers, though its proboscis is long enough to suck the latter normally;—sometimes it must at least attempt to suck the hermaphrodite flowers normally, for once (May 7, 1871) I saw a specimen sucking female flowers with pollen of *Nepeta* on its head; (12) *Apis mellifica*, L. ♀, sucking the female flowers normally; once (May 3, 1871) I saw it insert its head into several hermaphrodite flowers, but afterwards take to piercing the corolla with its maxillæ; (13) *Anthophora pilipes*, F. ♀ ♂ (19—21), very ab.; (14) *Osmia aenea*, L. ♀ (9—10) scarce; (15) *O. rufa*, L. ♀ ♂ (7—9), sucking both kinds of flowers normally; (16) *O. fusca*, Christ. ♀ (8); (17) *Nomada varia*, Pz. ♂

<sup>1</sup> *Forms of Flowers*, p. 304, etc.

above this, the tube suddenly widens, forming a pouch anteriorly, and its direction changes, becoming parallel to the stem. Very many short-lipped insects, especially flies and small bees, which are too small to effect cross-fertilisation, are thus excluded; for *Lamium album*, like so many of our native flowers with tubes 10 to 20 mm. long, is specially adapted for humble-bees and other large bees. The following characters of the corolla exemplify this. The erect part of the tube, which is 7 mm. long, is followed by the division of the tube into a bilobed lower lip (*b*, 1) which serves as a landing-place, two erect lateral lobes (*c*, 1) which admit the bee's head between them and are continued directly upwards from the side-walls of the tube, and the horizontal vaulted upper lip (*e*, 1) which serves to shelter the anthers (*f*, 1) and the stigmas (*g*, 1) immediately below it. The small appendages of the lateral lobes

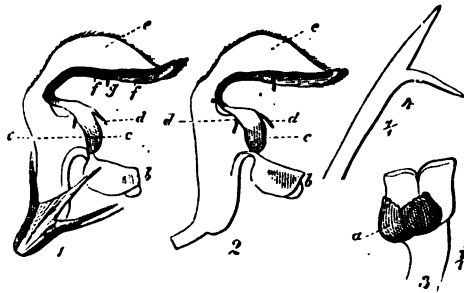


FIG. 167.—*Lamium album*, L.

- 1.—Flower, from the side.
  - 2.—Ditto, after removal of the calyx.
  - 3.—Ovary and nectary ( $\times 7$ ).
  - 4.—Tip of the style ( $\times 7$ ).
- a*, nectary; *b*, under lip; *c*, side-lobes which receive the bee's head between them; *d*, functionless appendages; *e*, upper lip; *f*, anthers; *g*, lower division of the style.

(*c*, 1) are functionless rudiments of the primitive five-lobed corolla. One of the divisions of the style which lies above or between the anthers lies in the same straight line with the style; while the other, a little shorter, bends downwards almost at right angles, so that its stigmatic tip projects below the anthers (4, Fig. 167). Cross-fertilisation is therefore induced, not by dichogamy, but by the position of the stigma. In absence of insects, self-fertilisation may take place, but it is doubtless rare, for the flowers are plentifully visited by bees.

We can estimate by direct observation how perfect the adaptation of this flower is to bees' visits. The bee alights on the under lip, and in doing so thrusts its head between the broad lateral lobes of the mouth, clings with its forefeet to the base

of the under lip, and with its mid and hindfeet to the two lobes of the under lip; then, if its proboscis is not less than 10 mm. long, it can at once reach the base of the flower. While sucking, the thorax, and in the case of small workers the base of the abdomen also, fills up the space between the upper and lower lips, and the vaulted upper lip fits the bee's back, which is pressed against the stigma and the open face of the anthers. These organs are often rubbed also by the bee's head as it enters the flower. In either case, the lower stigma gets touched before the anthers, and as the bees fly diligently from flower to flower, cross-fertilisation proceeds regularly.

The following observation shows how much this plant is visited by humble-bees in fine weather. One fine spring morning (May 17, 1868), while I was watching *Bombus agrorum* feeding on *Lamium album*, I observed that by the expansion and contraction of the bee's abdomen each separate act of sucking could be distinguished; and that it was possible to tell, when a bee began to suck, whether the flower was already exhausted of its honey. I found that between 9 and 10 A.M. a bee of the species *Bombus agrorum* abandoned four to five flowers on an average after a single taste before it found a flower on which it performed the act of sucking several (four to six or even eight to ten) times. By that early hour of the day four-fifths of all the flowers of this plant had been emptied of their honey.

Visitors : Hymenoptera—*Apidae* : (1) *Bombus agrorum*, F. ♀ ♀ (10—15); (2) *B. hortorum*, L. ♀ ♀ (18—21); (3) *B. silvarum*, L. ♀ (12—14); (4) *B. senilis*, Sm. ♀ (14—15); (5) *B. lapidarius*, ♂ ♀ (10—14); (6) *B. Scrimshiranus*, K. ♀ ♀ (10), creeping far into the flower; (7) *B. Rajellus*, Ill. ♀ (12—13); (8) *B. pratorum*, L. ♀ (11—12), all sucking normally, and sometimes brushing pollen off their backs into the pollen-baskets; (9) *B. terrestris*, L. ♀ (7—9), bites through the tube close above the calyx in open flowers and in nearly mature buds; (10) *Apis mellifica*, L. ♀ (6), only reaches the honey through holes bitten by *B. terrestris*; (11) *Anthophora pilipes*, F. ♀ ♂; (12) *Eucera longicornis*, L. ♂ (10—12); (13) *Melecta armata*, Pz. ♀ (12½), the last three sucking normally; (14) *Andrena nitida*, K. ♀ (3½), s., through the holes bitten by *B. terrestris*; (15) *Andrena albicans*, K. ♀; (16) *Halictus lævigatus*, K. ♀. I saw these last two collecting pollen; they seemed as likely to effect self-fertilisation as cross-fertilisation. B. Diptera—*Syrphidae* : (17) *Rhingia rostrata*, L., creeps a little way into the flower and inserts its tongue, without touching either stigma or anthers. See also No. 590, III., and No. 609.

*Leonurus Cardiacæ*, L., is visited by the hive-bee and by humble-bees (590, III.; 609).

fertilising flowers, the plant reproduces  
togamic flowers. These have been de  
(759) and Hildebrand (351).

360. *LAMIUM GALEOBDOLO*, Cra  
long, smooth in its lower, honey-holdin  
above; the entrance is expanded, and  
base of the flower though its proboscis is  
branches of the style are beset with ve  
do not increase in size, and they diverge  
soon after the flower opens. Cross-fert  
dichogamy but by the position of the pa  
lower division of the style lies somewh  
of the anthers, and hence if the bee's  
the anthers it escapes being touched;  
presses forcibly against the anthers, the  
contact with a different part of the bee  
ceive pollen from another flower than it  
of the lower stigma comes to project  
now regularly touched first by the  
on plants kept in the house, that, i  
pollen usually falls in the course  
stigma.

The visitors are exclusively bees.

- (1) *Bombus hortorum*, L. ♀ (21), ab.; (2)  
(3) *B. Rajellus*, Ill. ♀ (12—13); (4) *B. agrorum*

that supposing that a bee thrusts its head 5 mm. into the wide upper part, a proboscis 10 to 12 mm. long is needed to reach the honey.

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus hortorum*, L. ♂ ♀ (18—21), very ab., sucking normally; (2) *B. agrorum*, F. ♀ (12—15), do.; (3) *B. terrestris*, L. ♀ (7—9), bores through the corolla close above its bend, either piercing it with its maxillæ or biting a hole with its mandibles; (4) *B. Rajellus*, Ill. ♂ (10—11), steals the honey through holes bitten by *B. terrestris*. B. Diptera—*Syrphidae*: (5) *Rhingia rostrata*, L. (11—12), f.p., after trying in vain to reach the honey. See also No. 590, III.

362. *LAMIAM PURPUREUM*, L.—The tube is only 10 to 11 mm. long, and for the upper 4 to 5 mm. it is wide enough to admit the head of a small humble-bee. The hive-bee, though its proboscis is only 6 mm. long, is thus enabled to suck the honey. Sprengel calls the plant proterandrous; but in all the flowers which I have examined the stigmas and anthers developed simultaneously, though at first the angle between the two stigmas was less than it afterwards became, and the lower stigma stood at first above or between the anthers, but afterwards bent down below them. To decide whether the stigma is already capable of fertilisation when the flower opens, I set a plant of *L. purpureum* in a pot (April 26, 1871), and removed all the flowers and capsules already present on it. Next morning five flowers had just opened; in each I bent back the upper lip and the four anthers, and cut the latter off; I then placed upon the two stigmas (the lower of which received in this process some pollen of its own flower) pollen from freshly opened flowers of another plant, and I then marked my flowers with a spot of ink upon the calyx. The rest of the flowers I kept in my room, untouched and protected from insects. All the flowers were perfectly fertile. On May 21 the twenty nutlets of the five flowers which I had fertilised on April 27 had all fallen out, and I succeeded in finding them all. On June 8 I collected on the surface of the pot seventy-eight nutlets which had fallen from the self-fertilised flowers. *Lamium purpureum* is, therefore, certainly homogamous, and in default of insect-visits fertilises itself regularly.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♂ (6); (2) *Anthophora pilipes*, F. ♀ ♀ (19—21); (3) *Bombus hortorum*, L. ♀ (21); (4) *B. pratorum*, L. ♀ (11½); (5) *B. agrorum*, F. ♀ (12—15); (6) *Melecta armata*, Pz. ♀ (12½), all sucking in the normal way, and sometimes brushing off the pollen from their heads into their collecting-baskets; (7) *Halictus sexnotatus*, K. ♀ (4); (8) *H. cylindricus*, K. ♀ (3); (9) *H. leucopus*, K. ♀; these three try in vain to reach the honey, and abandon the plant after a few attempts. B. Diptera—*Bombylidae*: (10) *Bombylius major*, L. (10), s. See also No. 590, III.

363. *LAMIMUM INCISUM*, Willd. :—

Visitors : Hymenoptera—*Apidae* : (1) *Anthophora pilipes*, 21), ab. ; (2) *Bombus pratorum*, L. ♀ (11½) ; (3) *B. Rajellus*, Ill (4) *Apis mellifica*, L. ♀ (6), all sucking normally ; (5) *Halictus* K. ♀ (3), trying in vain to reach the honey.

364. *BALLOTA NIGRA*, L.—The corolla-tube is long ; above, it widens so little that a hive-bee cannot reach the anterior part of its head, and can just reach the flower with its proboscis, which is 6 mm. long. Near the base the tube is blocked by a ring of hairs, which permit the bee's proboscis to pass easily, but would suffice to exclude rain-drops, and are described



FIG. 168.—*Ballota nigra*, L.

- 1.—Essential organs of a young flower, viewed obliquely from the front.  
2.—Ditto, of an older flower.  
3.—Ovary (ov) and nectary (n).

as serving that purpose ; but as the horizontal position of the flower and its vaulted upper lip are sufficient protection against rain, their true use seems to be to exclude flies. Since bees proceed irregularly for the most part in visiting flowers, those whose proboscis is long enough to reach the honey (e.g. *Rhingia*, *Eristalis*, etc.) might rob many flowers of their honey without fertilising them ; but the ring of hairs is sufficient to prevent the expanded end of a fly's proboscis from entering the tube.

The under lip is marked with white guiding-lines towards the mouth of the tube ; its broad central lobe is the landing-place, the clefts between it and the lateral lobes are firm footholds for the forelegs and midlegs of the bee. The lateral lobes with the groove between them, bearing longitudinal ridges, guide the bee's proboscis.

Cross-fertilisation is favoured by the feebly-marked proterandrous dichogamy, and by the relative positions of stigma and anthers. At first, the divisions of the style lie close together behind the anthers (1, Fig. 168); afterwards, when the pollen is removed, they diverge more and bend down in front of and below the anthers (2, Fig. 168). In sunny weather bees' visits are so plentiful that all the pollen is removed before the stigmas diverge and bend downwards. During rainy weather, and in plants kept in the house, great part of the pollen as it escapes from the anthers remains adhering to the long woolly hairs which cover the under surface of the upper lip, and the inferior stigma curving downwards among these hairs becomes covered with the pollen of its own flower.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s. (6); (2) *Bombus Rajellus*, Ill. ♀ (12—13), s. and c.p.; (3) *B. silvarum*, L. (10—12), s.; (4) *B. lapidarius*, L. ♀ (10—12), s.; (5) *B. hypnorum*, L. ♀ (10—11), s.; (6) *B. muscorum*, F. ♀ (13—14), s.; (7) *B. (Apathus) rupestris*, F. ♀ (11—14), s.; (8) *Anthophora quadrimaculata*, Pz. ♀ ♂ (9—10), s. and c.p., very ab.; (9) *A. furcata*, Pz. ♀ ♂, s. and c.p., scarcer (Thur.); (10) *Osmia aurulenta*, Pz. ♀ (8—9), s. (Thur., Sld.); (11) *O. aenea*, L. ♀ (9—10), s.; (12) *O. fulviventris*, Pz. ♀, s. (Thur.); (13) *Anthidium manicatum*, L. ♀ ♂, wherever *Ballota* grows, very ab. in sunny weather, the females diligently collect pollen and suck honey, while the males buzz about and occasionally descend to suck honey on a flower; (14) *Megachile pyrina*, Lep. (*fasciata*, Sm.) ♀, s. B. Lepidoptera—(a) *Rhopalocera*: (15) *Argynnis Paphia*, L.; (16) *Vanessa urticae*, L. (12); (17) *V. cardui*, L.; (18) *Pieris brassicae*, L. (15); (19) *P. rapae*, L.; (20) *Colias hyale*, L.; (b) *Sphinges*: (21) *Macroglossa stellatarum*, L.; all these Lepidoptera were sucking; the specimens I caught had their tongues dusted with pollen and were probably effecting fertilisation. See also No. 599, III.

In *Prostanthera*, Labill., long two- or three-toothed appendages of the connectives come in contact with the insect and cause shedding of the pollen (178, 360).

365. *TEUCRIUM SCORODONIA*, L., is markedly proterandrous.<sup>1</sup> When the flower opens, the stamens protrude from it, lying close to the superior wall of the tube, and continuing in a line with it, or bending slightly forwards. The two divisions of the style are already separate but stand behind the stamens so that they escape being touched by the head of a bee visiting the flower; the anthers, which dehisce inferiorly by a longitudinal slit, shed their

<sup>1</sup> The proterandry of *Teucrium* and the movements of its reproductive organs have been described by Delpino, No. 178, Hildebrand, No. 360, pl. x., and Ogle, No. 632.

with pollen.

Honey is secreted by the tissue below the corolla-tube. Labiates that I have examined (cf. Fig. 168) find that the corolla-tube (which is 9 to 10 mm. long) extends to a depth of 4 mm. The flowers are



FIG. 169.—*Teucrium Scorpioides*.

- 1.—Flower, in first (male) stage ( $\times 10$ ).
- 2.—Ditto, at the beginning of the second stage ( $\times 10$ ).
- 3.—Ditto, at the end of the second stage ( $\times 10$ ).

aggregation, and in spite of their dull coloration are visited by insects as to be able to dispense with fertilisation.

Visitors : A. Hymenoptera—*Apis* : (1)

*Teucrium Chamædrys*, L., is proterandrous; the movements of the reproductive organs are similar to, but feebler than, those of *T. Scorodonia*. The visitors are bees, and a proboscis 7 to 10 mm. long is requisite to reach the honey (609).

*Teucrium Botrys*, L., is visited by species of *Anthidium* (590, III).

366. *AJUGA REPTANS*, L.—The tube is 9 mm. long, and is expanded for  $2\frac{1}{4}$  mm. at the base; the lower expanded part is white, and full of honey, which is secreted by a thick, yellow, fleshy gland below the ovary on the side turned towards the under lip. The upper lip is absent, but the protruding anthers of each flower are sheltered by the bract of the flower above. When the flower opens, the two stigmas diverge to their full extent and their papillæ are already mature. Cross-fertilisation is favoured not by dichogamy but by the position of the organs. For in young flowers the lower division of the style, provided at its tip with stigmatic papillæ, rests upon the shorter stamens which lie close together, and is protected by them from contact with the bee visitors, at least in the case of the smaller bees which do not force the stamens much apart; while all the anthers turn their pollen-covered faces forwards and downwards so as to touch all insect-visitors. Afterwards the inferior stamens separate, the style loses their support, and its lower division, with the stigmatic tip turned downwards and forwards, projects between the anthers, and is touched before them by the bee.

In absence of insects, the pollen remains adhering to the lower surface of the anthers in large masses, which readily come in contact with the stigma and effect self-fertilisation.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀ (6), thrusts the greater part of its head into the tube; (2) *Bombus lapidarius*, L. ♀ (12—14); (3) *B. agrorum*, F. ♀ (12—15); (4) *B. confusus*, Schenck, ♀ (12—14); (5) *B. muscorum*, F. ♀ (13—14); (6) *B. pratorum*, L. ♀ (8); (7) *B. silvarum*, L. ♀ (12—14); (8) *B. hortorum*, L. ♀ ♀ (18—21); (9) *Anthophora pilipes*, F. ♀ ♂ (19—21); (10) *Osmia rufa*, L. ♂ (7—8); (11) *O. ænea*, L. ♀ (9—10); (12) *O. fusca*, Christ. (=bicolor, Schrk.), all sucking normally and dusting their heads with pollen; (13) *Andrena nitida*, Fourc. ♀ (3½); (14) *A. labialis*, K. ♂; (15) *Halictus zonulus*, Sm. ♀ (4); these three are unable to reach the honey, and abandon the plant after visiting a few flowers. B. Diptera—*Syrphidae*: (16) *Rhingia rostrata*, L. (11—12), usually s. and f.p. on the same flower, while sucking it dusts its head with pollen. C. Lepidoptera—(a) *Rhopalocera*: (17) *Pieris brassicæ*, L. (15); (18) *P. napi*, L.; (19) *P. rapæ*, L.; (20) *Rhodocera rhamni*, L. (15—16); (21) *Papilio Podalirius*, L.; (22) *Hesperia*

pollen on the bee's head. Gradually the filaments bend backwards (2, 1, Fig. 169) out of the bee's way, while the two stigmas spread more and more apart, bending slightly forwards into the place where the anthers were before. In absence of insects, self-fertilisation rarely takes place, for the stamens as a rule do not touch the stigmas; yet in a good many flowers the anthers come in contact with the stigmas in bending backwards, and dust them with pollen.

Honey is secreted by the tissue below the ovary, as in all the Labiates that I have examined (cf. Fig. 168, 3), and so plentifully that the corolla-tube (which is 9 to 10 mm. long) is often filled to a depth of 4 mm. The flowers are rendered conspicuous by



FIG. 169.—*Teucrium Scorodonia*, L.

- 1.—Flower, in first (male) stage ( $\times 3\frac{1}{2}$ ).
- 2.—Ditto, at the beginning of the second (female) stage.
- 3.—Ditto, at the end of the second stage.

aggregation, and in spite of their dull colour they are so abundantly visited by insects as to be able to dispense with the power of self-fertilisation.

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus pratorum*, L. ♀ ♀ (8—11½, s., very ab.; (2) *B. agrorum*, F. ♀ ♀ (10—15), do.; (3) *B. hypnorum*, L. ♂ (10), s.; (4) *Anthophora quadrimaculata*, Pz. ♀ (9—10), s.; (5) *Saropoda bimaculata*, Pz. ♀ ♂ (9), very ab., s. B. Diptera—*Syrphidae*: (6) *Eristalis nemorum*, L., f.p., and thus only able to effect fertilisation occasionally. It is noteworthy that the honey-bee (whose proboscis is 6 mm. long), was not observed on this abundantly nectariferous flower. It would be just able to taste the honey. See also No. 590, III.

According to Dr. Buchanan White, *Teucrium Scorodonia* is visited by many nocturnal Lepidoptera (773).

*Teucrium Chamædrys*, L., is proterandrous; the movements of the reproductive organs are similar to, but feebler than, those of *T. Scorodonia*. The visitors are bees, and a proboscis 7 to 10 mm. long is requisite to reach the honey (609).

*Teucrium Botrys*, L., is visited by species of *Anthidium* (590, III).

366. *AJUGA REPTANS*, L.—The tube is 9 mm. long, and is expanded for  $2\frac{1}{2}$  mm. at the base; the lower expanded part is white, and full of honey, which is secreted by a thick, yellow, fleshy gland below the ovary on the side turned towards the under lip. The upper lip is absent, but the protruding anthers of each flower are sheltered by the bract of the flower above. When the flower opens, the two stigmas diverge to their full extent and their papillæ are already mature. Cross-fertilisation is favoured not by dichogamy but by the position of the organs. For in young flowers the lower division of the style, provided at its tip with stigmatic papillæ, rests upon the shorter stamens which lie close together, and is protected by them from contact with the bee visitors, at least in the case of the smaller bees which do not force the stamens much apart; while all the anthers turn their pollen-covered faces forwards and downwards so as to touch all insect-visitors. Afterwards the inferior stamens separate, the style loses their support, and its lower division, with the stigmatic tip turned downwards and forwards, projects between the anthers, and is touched before them by the bee.

In absence of insects, the pollen remains adhering to the lower surface of the anthers in large masses, which readily come in contact with the stigma and effect self-fertilisation.

Visitors: A. Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♂ (6), thrusts the greater part of its head into the tube; (2) *Bombus lapidarius*, L. ♀ (12—14); (3) *B. agrorum*, F. ♀ (12—15); (4) *B. confusus*, Schenck, ♀ (12—14); (5) *B. muscorum*, F. ♀ (13—14); (6) *B. pratorum*, L. ♀ (8); (7) *B. silvarum*, L. ♀ (12—14); (8) *B. hortorum*, L. ♀ ♂ (18—21); (9) *Anthophora pilipes*, F. ♀ ♂ (19—21); (10) *Osmia rufa*, L. ♂ (7—8); (11) *O. ænea*, L. ♀ (9—10); (12) *O. fusca*, Christ. (= *bicolor*, Schrk.), all sucking normally and dusting their heads with pollen; (13) *Andrena nitida*, Fourc. ♀ (3 $\frac{1}{2}$ ); (14) *A. labialis*, K. ♂; (15) *Halictus zonulus*, Sm. ♀ (4); these three are unable to reach the honey, and abandon the plant after visiting a few flowers. B. Diptera—*Syrphidae*: (16) *Rhingia rostrata*, L. (11—12), usually s. and f.p. on the same flower, while sucking it dusts its head with pollen. C. Lepidoptera—(a) *Rhopalocera*: (17) *Pieris brassicæ*, L. (15); (18) *P. napi*, L.; (19) *P. rapæ*, L.; (20) *Rhodocera rhamni*, L. (15—16); (21) *Papilio Podalirius*, L.; (22) *Hesperia*

alveolus, H ; (b) *Sphinges* : (23) *Macroglossa fuciformis*, L. (Stromberg), all sucking. See also No. 590, III.

*Ajuga pyramidalis*, L., is said by Ricca to be homogamous (665); I have found it slightly proterandrous, and visited by humble-bees (609).

*Ajuga genevensis*, L.—The flowers are larger than those of *A. pyramidalis*, and the nectary is very large. The plant is visited by humble-bees and by Lepidoptera. A proboscis 7 to 8 mm. long is requisite to reach the honey (609).

#### REVIEW OF THE LABIATÆ.

Delpino mentions the following six points as characteristic of the flower in Labiatæ (178).

(1) The horizontal position of the axis of the flower. (2) Division of the corolla into upper and lower lips. (3) Union of two petals in the upper lip, three in the lower. (4) Position of anthers and stigma below the vaulted upper lip, which shelters them. (5) Position of the nectary at the base of the flower below the lower lip, whose anterior part forms a platform for insects. (6) Well-marked dichogamy ("*deciso asincronismo nello sviluppo degli organi sessuali*") (Delpino, No. 178, p. 128; Hildebrand, No. 360).

But this summary is only correct if we call only those Labiates typical to which it directly applies; it requires most important modifications if it is to hold good for the majority of Labiates. For (1) the axis of the flower is never or hardly ever truly horizontal, but, as a rule, is rather bent into the curve most convenient for long-tongued bees (*Lamium*, *Galeobdolon*, *Galeopsis*, *Betonica*, etc.). (2) The upper lip is entirely absent in many cases (*Ajuga*, *Teucrium*), bracts belonging to the flowers above taking its place in sheltering the stamens from rain. (3) The under lip is by no means always formed of three petals, but in *Lamium*, for instance, consists of one only; the two lateral petals have here assumed a special function, forming two erect lobes which receive the bee's head between them. (4) The stamens project beyond the corolla not only in *Ajuga* and *Teucrium*, where the upper lip is absent, but also in *Thymus*, *Lycopus*, *Mentha*, etc., and the stigma also projects beyond the corolla in *Salvia*. (5) The fifth statement is correct for the great

majority, *Plectranthus*, *Ocimum*, *Salvia patens*, etc., being exceptions to it. (6) Dichogamy has been shown above to be far from universal: *Ajuga*, *Lamium*, *Galeopsis*, and others are homogamous, and even in the majority of the others dichogamy is not so complete as to prevent self-fertilisation. Self-fertilisation seems to be rendered impossible only in the species of *Nepeta*, *Thymus*, *Mentha*, and *Salvia* described above.

In regard to the insects which the Labiatae have adapted themselves to, the forms which I have described show a remarkable series of gradations, the visitors being more and more restricted as the length of the corolla-tube increases.

The short-tubed flowers of *Mentha* and *Lycopus* are visited chiefly by flies and also by insects of various other orders. In *Thymus* and *Origanum*, in addition to flies, bees come more and more to the front, though insects of other orders take a certain share; in *Betonica* bees and flies are of about equal importance as fertilisers; in *Stachys palustris* and *S. silvatica* bees are very much the most important visitors, and in *Lavendula*, *Salvia*, *Galeobdolon*, *Lamium*, *Galeopsis*, *Ballota*, *Teucrium*, and *Ajuga* bees perform almost all the work of fertilisation, though *Lepidoptera* and long-tongued flies are not excluded.

#### ORD. PLANTAGINEÆ.

367. *PLANTAGO LANCEOLATA*, L.—Delpino (567) distinguishes three forms of this species:—

“One form,” he says, “with a strong and very tall scape, and very broad, white anthers which quiver in the wind, grows in meadows and is exclusively anemophilous, for I have never seen it visited by insects. The second form grows on the hills, and has a much shorter scape; it also is essentially anemophilous; I once saw a species of *Halictus* on a spike, trying to gather pollen; but the structure of the flower is so unfitted for pollen-collecting, that great part of the pollen fell to the ground without benefiting either the plant or the insect. Finally, the third form is dwarfish and confined to the mountains; it has the shortest spikes and filaments; on meadows in the Apennines at Chiavari I have seen bees in numbers flying from one flower to another of this variety, collecting the pollen and performing cross-fertilisation.

“This therefore is a form of *Plantago* which hangs between the anemophilous and entomophilous conditions, and is capable of being fertilised equally well by the wind and by bees. If the filaments became stiff and coloured and the pollen-grains adhesive while the anthers lost their peculiar quivering, we should have before us the passage from anemophilous to entomophilous characters, the evolution of an entomophilous from an anemophilous species.

“This hypothetical transition has actually occurred. *Plantago media* is a

form that has become entomophilous; the filaments have become pink, the anthers are motionless, the pollen-grains have become more aggregated, and it is visited regularly by *Bombus terrestris*, as I have observed at the same spot (Chiavari) in the Apennines."

I have transcribed this passage in order to induce botanists in as many places as possible to observe the forms of this species with reference to its adaption for insect-visits.

In the neighbourhood of Lippstadt I have caught pollen-collecting bees and pollen-feeding flies both on plants with tall.

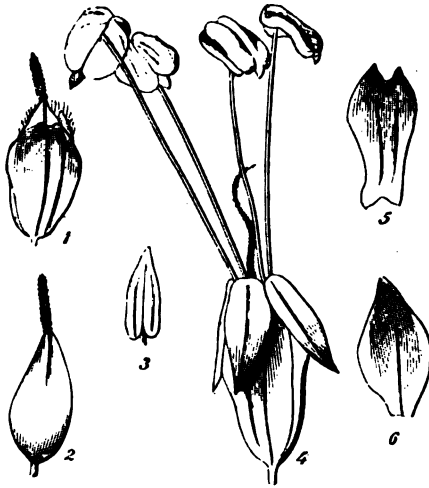


FIG. 170.—*Plantago lanceolata*, L.

- 1.—Flower, in first (female) stage. The petals and stamens are still within the bud.
- 2.—Ditto, after removal of the calyx.
- 3.—An anther from this flower.
- 4.—Flower, in second (male) stage.
- 5.—The two inferior coherent sepals.
- 6.—A lateral sepal.

scapes and long spikes and on those with short scapes and spikes; and in neither form have I found the least trace of adaptation to insect-visits. Delpino's account is not minute enough to permit a correlation of his plants with those of other localities, and it is quite possible that the varieties which he has observed do not occur at Lippstadt.

It is just possible that Delpino has been led into imagining adaptations which have no real existence by the success which the honey-bee attains in gathering pollen, chiefly owing to its plan of smearing the pollen with honey. The two extreme forms of *P.*

eight stamens. The five which are constantly present alternate with the parts of the perianth; the other three stand opposite to the parts of the perianth. At the base of each perianth-segment is a nectary, secreting very scanty honey, which remains in a moist adhesive layer. The ovary is generally bilateral, bearing a style which divides into two branches, each bearing a stigmatic knob; but three stigmatic branches often occur. Anthers and stigmas ripen together and stand at the same level. The flower expands until the perianth forms an almost hemispherical cup, and the five stamens alternating with the perianth-segments spread out as far as the perianth allows. The stigmas are, therefore, seldom or never touched by these stamens, but the other three stamens, when present, bend towards the middle of the flower and come in contact with the stigmas. Now although, as in

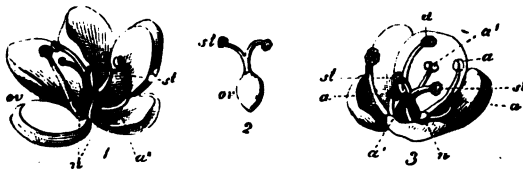


FIG. 174.—*Polygonum Persicaria*, L.

- 1.—Flower with five stamens.
  - 2.—Pistil.
  - 3.—Flower with seven stamens.
- a, five outer anthers; a', inner anthers; a', rudimentary filament;  
ov, ovary; st, stigma; n, nectary.

*P. fagopyrum*, the five outer anthers shed their pollen inwards and the three others outwards, self-fertilisation takes place regularly in all flowers with more than five stamens, since the anthers dehisce so widely as to be covered with pollen all round. Whether flowers with only five stamens fertilise themselves in absence of insects I cannot say from direct observation; but they probably do so, as almost all the flowers of *P. Persicaria* develop seed, in spite of the scanty insect-visits. The flowers, as I have often seen, remain expanded even in rain, and self-fertilisation in flowers with five stamens can only take place at the end of the flowering period, when the perianth closes up and brings stigmas and stamens into contact.

The small size of the flower causes every insect that inserts its head to touch one or two stamens and a stigma. If the insect thrusts its proboscis once into each flower, cross-fertilisation must

and creeps upwards. Since the scattered pollen in part reaches the stigmas of the same or neighbouring plants, we have here anemophilous flowers fertilised also by insects." (2) *Bombus pratorum*, L. ♀, c.p. ; (3) Small sp. of *Halictus*, busy about the anthers. B. Diptera—*Syrphidae* : (4) *Melanostoma mellina*, L., very ab., f.p. ; (5) *Syrphus ribesii*, L., f.p., freq. ; (6) *Volucella pellucens*, L., f.p. Whenever I have examined bees caught on *P. lanceolata* I have always found numerous pollen-grains among the feathered hairs. See also No. 590, III.

Darwin found *P. lanceolata* to be gynodioecious in England (167).

*Plantago alpina*, L.—The stigma does not wither until after the ripening of the anthers, so that the plant retains the power of self-fertilisation. The limb of the corolla, and sometimes the borders of the sepals, are red, which is perhaps an adaptation favouring insect-visits. The tendency towards homogamy is probably also brought about by insect-visits, as the insects come only for the sake of pollen, and therefore seek only flowers with ripe anthers (No. 609, fig. 139).

368. *PLANTAGO MEDIA*, L.—While I have been unable to find any trace of adaptation to insect-visits in the various forms of *P. lanceolata*, specimens of *P. media* which I have examined seem to show such traces in the reddish colouring of the filaments and the pleasant perfume of the plant. Nevertheless, in all the forms of this species the filaments are so long, thin, and freely motile, the anthers so broad, and the pollen-grains so smooth and dry, that wind-fertilisation can be effected very readily. *P. media*, therefore, is truly intermediate between the anemophilous and entomophilous conditions.

In the neighbourhood of Lippstadt *P. media* exhibits variability such as Delpino describes in the case of *P. lanceolata*. It seems remarkable that the form *A*, which I have observed on dry sunny road-sides, is adapted in a less degree for insect-visits than the form *B*, which grows in more shady spots ; but I must add that a form agreeing essentially with *B*, but much taller, grows on the sunny slopes of the canal-embankment at Lippstadt, and is much visited by insects there.

The form *A* has a scape 8 to 12 inches in length, and a spike about 40 mm. long, increasing during the flowering period to 70 or 80 mm. The filaments, which are bent down slightly by the weight of the anthers, are white, and protrude for 7 to 9 mm. from the flower ; the lobes of the corolla are acute and outspread ; the

stigmas protrude far beyond the flower. The form *B* on the other hand has a scape about 6 inches long, and shorter reddish filaments which do not bend under the weight of the anthers; the lobes of the corolla are rounded, and do not spread apart but only point obliquely upwards, and the stigmas protrude little from the flower. The pollen in both forms is powdery, but is slightly more adhesive in the second form (*B*), as may be seen by the filaments in this form being usually covered thickly with pollen-grains.

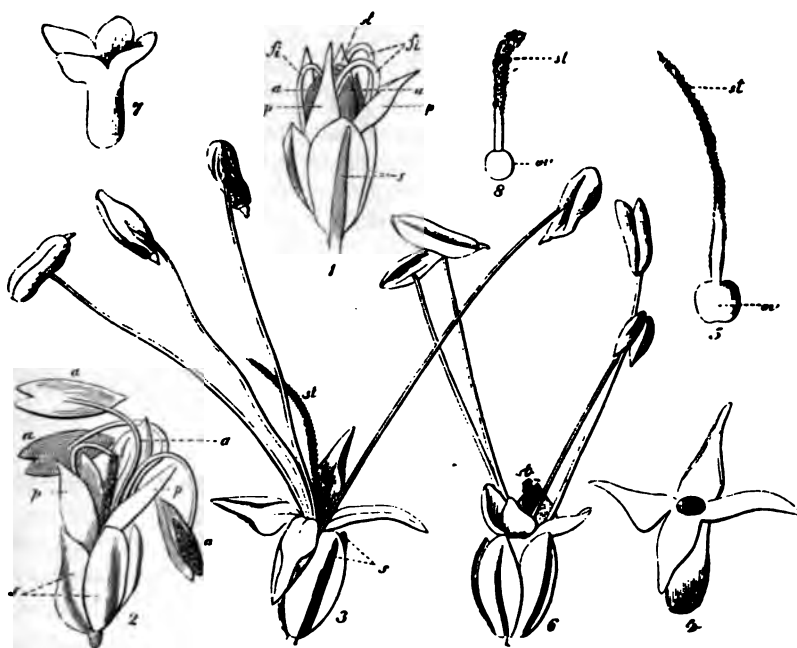


FIG. 171.—*Plantago media*, L.

- A.* 1–5.—A form of *P. media* from dry sunny slopes on Rixbecker Hill, near Lippstadt.  
 1, bud; 2, developing flower; 3, fully developed flower; 4, corolla; 5, pistil.  
*a*, sepal; *p*, petal; *s*, anther; *st*, stigma.  
*B.* 6–8.—Another form of *P. media*, growing in damp shady spots on the same hill, often within a few paces of the other.  
 6, fully developed flower; 7, corolla; 8, pistil.

The form growing on the slopes of the canal-embankment, from which I have chiefly compiled my list of insect-visitors, has a scape 10 to 14 inches long, a spike 35 to 90 mm. long, and stamens which project only 4·5 to 7 mm. beyond the flower; in the form and development of the corolla and style and in the nature of the pollen it agrees well with the form *B* from the Rixbecker Hill.

## REVIEW OF THE SPECIES OF POLYGONUM.

The species of *Polygonum*, like those of *Geranium*, show clearly how with conspicuousness and abundance of honey the number and variety of visitors increase, and how, as the likelihood of cross-fertilisation is thus increased, the possibility of self-fertilisation becomes less important; the converse is also clear. But they show at the same time that the abundance of a plant is in no way determined alone by the certainty of cross-fertilisation.

*P. fagopyrum* and *P. Bistorta* have the most conspicuous flowers, the most abundant honey, and the most numerous visitors; in both, cross-fertilisation is insured and self-fertilisation rendered difficult or impossible,—in the former species by dimorphism, in the latter by well-marked proterandrous dichogamy. *P. Persicaria* and *P. lapathifolium* have much smaller flowers and scantier honey; but, by union of their flowers in a spike, they become fairly conspicuous and attract fairly numerous visitors; both waver between insuring cross-fertilisation and insuring self-fertilisation, and seem to make use, to a great extent, of both processes. In *P. minus* the flowers are about as large and rich in honey as those of *P. Persicaria*, but are united in much looser, thinner spikes; they are therefore less conspicuous, less visited by insects, and more subject to self-fertilisation. Finally, in *P. aviculare*, whose flowers are not only much smaller, but are solitary and devoid or almost devoid of honey, insect-visits and consequent cross-fertilisation are only the exception; yet this species is with us the most abundant of its genus, and one of the commonest of our native plants.

The species of *Rumex* are anemophilous, and Axell figures the flowers of *Rumex crispus* to compare them with the entomophilous flowers of *Rheum Rhaponticum*; I have however found a bee, *Halictus cylindricus*, F. ♀, busily engaged upon the anthers of *Rumex obtusifolius*, L.; and in the Alps I have often seen red butterflies seated on *Rumex* when in seed and like them in colour (590, II.; 609).

## ORD. CYTINACEÆ.

*Brugmansia Zippelii*, Blume, is fertilised, in Delpino's opinion, by carrion-flies which are detained for a time in the flowers (178).

## ORD. ILLECEBRACEÆ.

*Illecebrum verticillatum*, L., has submerged anisogamous flowers (351).

*Herniaria glabra*, L.—The flowers are very inconspicuous, and are visited by minute insects (590, II.).

*Scleranthus perennis*, L.—The small inconspicuous flowers have no petals; the sepals, which are white at the edges, take the place of a corolla; the honey, which is secreted in the lower half of the calyx, is accessible to short-lipped insects. Anthers and stigmas ripen together, and the widely outspread position of the stamens favours cross-fertilisation. I have found *Zeugophora coriaceum*, Dhlb. (*Chrysida*), sucking honey in the flowers.

## ORD. AMARANTACEÆ.

*Chamissoa* affords an example of the passage from a dimorphic to a diclinous condition (555).

## ORD. CHENOPODIACEÆ.

*Chenopodium ambrosioides* is figured by Hildebrand as an example of a self-fertilised plant (351).

*Chenopodium album*, L., is anemophilous, but is visited by pollen-eating Syrphidæ (*Melanostoma mellina*, L.) (590, II.).

*Chenopodium bonus-Henricus* is protogynous according to Warming (762).

## ORD. POLYGONACEÆ.

369. *Polygonum fagopyrum*, L.—The flowers are made conspicuous by their white or red perianth, by aggregation, and by their perfume. Eight rounded yellow glands at the base of the stamens secrete honey, which lies at the bottom of the shallow outspread perianth; it is accessible to short lipped insects, and attracts great numbers of insects of different orders.

Three stamens, with their pollen covered sides turned outwards, stand close round the styles in the middle of the flower: five, with their pollen-covered sides directed inwards, stand round the circumference. The eight nectaries lie at the bottom of the flower between the inner and outer stamens, so that insects must come between these to reach the honey, and hence get dusted with

376. *ARISTOLOCHIA SIPHO*, L. (178, 349, 360).—In this species the corolla maintains the same position during the whole period of flowering. Its lower part is directed straight downwards, and then with a sudden bend turns directly upwards; it is moderately wide, and the mouth is provided with a three-lobed lip. In this species, as in the previous one, we find flies imprisoned during the first stage, while the stigmas alone are ripe; they fertilise the stigmas with pollen brought from other flowers, and remain caged until the stigmas wither and the anthers shed their pollen.

The reason why they stay imprisoned so long seems to me still insufficiently explained. In Delpino's opinion, to which Hildebrand assents, the smooth sides of the tube prevent the flies creeping up, until the withering of the flowers affords them foothold. This explanation can only be correct if that part of the tube which slopes downwards from the entrance is distinctly smoother than the other portion which leads up from the lowest part of the tube to the expanded terminal chamber; for if both are equally smooth the flies will have as much difficulty in climbing up into the stigmatic chamber as in climbing back out of the flower. In *Arum* I have repeatedly noticed that the small midges try to escape from their prison, not by creeping, but by flying towards the light, and get knocked down by the grating at the mouth of the flower. So if in *Aristolochia Sipho* the inside of the tube is all so smooth that flies can climb neither one way or the other from the lowest part, the reason of their imprisonment must be sought only in the curvature of the two ends of the tube, the one rising straight from the lowest part to the cage, while the other part which rises up towards the entrance of the flower is so bent outwards at its upper end that the insects flying towards the light knock against the bend and fall back again. They are set free by the shrivelling up of the corolla, which enables them to creep out.

Delpino found in the cage: (*a*) *Muscidæ*: (1) *Lonchæa tarsata*, Fallen; (*b*) *Phoridæ*: (2) *Phora pumila*, Mgn. I found: *Muscidæ*: (1) *Sapromyza apicalis*, Loew, very ab.; (2) *Myodina fibrans*, L., scarce; also a small black gnat, very ab., which I was unable to identify.

*Aristolochia altissima*, Dsf., *A. rotunda*, L., and *A. pallida*, W., show only slight variations from *A. Clematidis*, according to Delpino (178).

*A. Bonplandi*, Ten., unites the form of corolla of *A. Sipho* with a transitory hairs of *A. Clematidis* (360).

(16) *Athalia spinarum*, F., s. B. Diptera—(a) *Syrphidæ*: (17) *Eristalis tenax*, L.; (18) *E. pertinax*, Scop.; (19) *E. nemorum*, L.; (20) *E. arbustorum*, L.; (21) *E. sepulcralis*, L.; (22) *E. intricarius*, L.; all ab., s. or f.p.; (23) *Helophilus florens*, L.; (24) *Syritta pipiens*, L.; (25) *Chrysotoxum festum*, L.; (26) *Melithreptus scriptus*, L.; (27) *M. tæniatus*, Mgn.; (28) *Syrphus pyrastris*, L.; (29) *Pipiza funebris*, Mgn.; (30) *Cheilosia scutellata*, Fallen; (b) *Muscidæ*: (31) *Pollenia Vespillo*, F.; (32) *Musca corvina*, F.; (33) *Lucilia cornicina*, F.; (34) *Sarcophaga carnaria*, L.; (c) *Stratiomyidæ*: (35) *Odonotomia viridula*, F.; (36) *Stratiomys Chamæleon*, Deg., ab.; (37) *Str. riparia*, Mgn.; most of these flies sucking, the *Syrphidæ* also eating pollen. C. *Lepidoptera*—(38) *Vanessa urticae*, L.; (39) *Pieris brassicae*, L.; (40) *P. napi*, L.; (41) *Polymmatas Phloceas*, L., all s.

370. *POLYGONUM BISTORTA*, L.—As in *P. fagopyrum*, the flowers are made conspicuous by aggregation and by their coloured

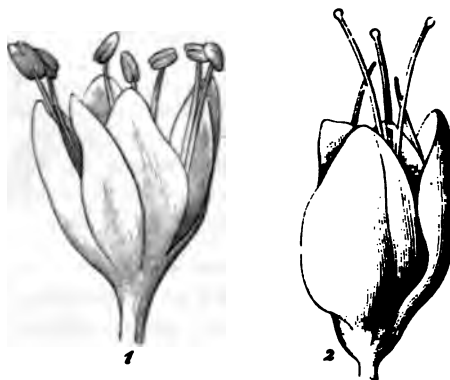


FIG. 173.—*Polygonum Bistorta*, L.

1.—Flower, in first (male) stage.

2.—Ditto, in second (female) stage.

perianth; eight red swellings at the base of the stamens secrete honey, which lies freely open at the bottom of the flower. The power of self-fertilisation has been lost; but while in *P. fagopyrum* crossing has been insured by the development of long-styled and short-styled stocks, in *P. Bistorta* the same end has been gained by complete proterandrous dichogamy. In the first stage, the anthers protrude freely from the flower, which never expands very widely; afterwards, when the anthers are withered and mostly fallen off, the ends of the styles with their stigmas protrude.

On the meadows at Brilon, I saw the flowers plentifully visited by flies, but I was busy with other observations and can name only the following easily recognised forms: *Rhingia* ~~rust~~

ORD. *ELÆAGNEÆ*.

*Elæagnus angustifolia*, L., is visited by *Apis mel* and *Syrhitta pipiens* (Syrphidæ) (590, II.).

ORD. *SANTALACEÆ*.

*Thesium alpinum*, L., is homogamous (609, fig. 154)  
*Thesium pratense*, Ehrh., is visited by the hive-bee (

ORD. *EUPHORBIACEÆ*.

The regular branching and the order of succession of flowers in *Euphorbia helioscopia* has been thoroughly described by Delpino. He states that Euphorbiaceæ are fertilised (178, 360).

This, however, is not altogether correct. Very nectar-sucking insects (flies, beetles, Hymenoptera) resort to exposed honey and aid in the work of cross-fertilisation. If *Euphorbia* is growing in abundance even bees resort to it. I have found upon *E. Cyparissius* in Low Germany:—Coleoptera, 8; Hemiptera, 3; Hymenoptera, 10 (Apididoptera, 1 (590, II.). On the same plant I have found in the Alps:—21 flies; 1 beetle; 4 Hymenoptera, of which 3 are bees; and 3 Lepidoptera (609).

*Euphorbia (Poinsettia) pulcherrima* has scarlet bracts and a large nectary in each (726).<sup>1</sup>

A Brazilian species of *Dalechampia*, according to Engelm., attracts the insects which cross-fertilise it by means of resin secreted in special glands. This is collected by bees, and used in nest-building (597).

ORD. *URTICACEÆ*.Tribe *Urticeæ*.

The plants of this tribe are anemophilous; the stamens fall when the flower opens, scattering the pollen (178).

*Parietaria* has protogynous flowers (351).

<sup>1</sup> Lists of visitors to the following Euphorbiaceæ are given in: *Euphorbia Esula*, L., *E. Gerardiana*, Jacq., *E. peplus*, L., *E. helioscopia*, L., *E. sempervirens*, L.

*Urtica urens*, L., owes its great abundance to the early period of the year at which it flowers, its regular cross-fertilisation, and the quick ripening of its fruit (590, 597).

Tribe *Artocarpeæ*.

377. *FICUS CARICA*, L.—The latest researches confirm the fact, which Linnæus (416A) was aware of, that the so-called *Caprificus*, which bears inedible fruit, and the fig-tree, cultivated for the sake of its fruit from time immemorial, stand in the relation of male and female to one another. Fertilisation is effected by a wasp, *Blastophaga grossorum*, Grav. (*Cynips Pscnes*, L., *Chalcididæ*). The hollow inflorescence which we call a fig is very markedly protogynous in both the fig-tree and the *Caprificus*. The greater part of its inner wall is covered with female flowers, which are mature when the "eye" (*ostiolum*) of the young fig opens. Male flowers line a limited zone near the orifice, and are not mature until the fig is ripe. The *Caprificus* produces three crops of figs annually, one crop beginning to flower as the previous one is ripe. Many varieties of the fig-tree ripen two crops, some three, annually. In most cases each crop of figs, whether of the fig-tree or the *Caprificus*, brings only flowers of one sex to full maturity.

At Naples, the *Caprificus* ripens its three crops of inedible figs in April, June, and August. The first crop are called *mamme*, the second *profichi*, and the third *mammoni*. Each of these hatches a new generation of fig-wasps, but it is only the second which produces the pollen with which the fig-tree is cross-fertilised. Each crop produces female flowers in which the wasps undergo their development, but male flowers are usually quite wanting in the *mamme*, few in number in the *mammoni*, and only plentiful in the *profichi*. The fig-tree also produces three crops in the season, called *fiori di fico*, *pedagnuoli*, and *cimaroli*.

The reproduction of the fig-wasp takes place in the following way. The female wasps force their way with the loss of their wings into young figs of the *Caprificus*, through the narrow ostiolum. They lay their eggs in the ovaries of the female flowers, between the nucleus and the integuments, placing one egg only in each. The wasp dies within the fig to which it has intrusted its offspring. In consequence of the puncture which the wasp has made, the female flower enlarges after the manner of a gall, and in its ovary instead of its own embryo, the wasp-embryo develops. While the figs themselves are protogynous, the wasps on the other hand are proterandrous. The wingless males are the first to

emerge; they gnaw their way into the ovaries in which the females lie, and impregnate them, and afterwards perish within the same fig in which they were born. The winged females then escape by widening the passage made by the males. They leave the ripe fig by way of the ostium, and enter a young fig either of the same *Caprificus* or of a neighbouring fig-tree, to lay their eggs in its female flowers. The wasps which enter the young *Caprificus*-figs (either passing from *mamme* to *profichi*, or from *profichi* to *mammoni*, or from *mammoni* to *mamme*) produce a new progeny; those on the other hand which enter young figs upon a fig-tree (passing from *mamme* to *fiori di fico*, or from *profichi* to *pedagnuoli*, or from *mammoni* to *cimaruoli*) leave no offspring, since in the cultivated figs the female flowers are so constituted that the wasps are not able to lay their eggs in the right spot.

Of the three generations of wasps only those which have developed within *profichi* act as fertilising-agents. In the *profichi*, at the time when the wasps escape from the ovaries, the zone of male flowers near the ostium is covered with pollen; so the wasps leave these figs laden with pollen. They carry this pollen partly to the stigmas of young *mammoni* of *Caprificus*, which, however, rarely set a seed capable of germinating, and partly to the *pedagnuoli* of the fig-tree, which after this cross-fertilisation bear good seed plentifully.

While the fruit of the *Caprificus*, whose only use is to supply pollen, remains hard and withers on the tree or falls off without becoming sweet, the fruit of the fig-tree, when the seeds ripen, becomes sweet and juicy, and so attracts birds which disseminate the seeds.

From the most ancient times, as long as the fig-tree has been cultivated, its artificial fertilisation by means of the *Caprificus*, or so-called *Caprification*, has been practised. This process consists in hanging ripe fruit of the *Caprificus* (*profichi*) to the branches of fig-trees, whose figs (*pedagnuoli*) are then in their female stage, with open ostia. The wasps, issuing from the former, enter the latter, bringing the pollen of the *profichi* with them.<sup>1</sup>

*Sycomorus antiquorum*, Miq.—The Egyptian Sycamore has for its fertilising agent a small wasp, *Sycophaga sycomori*, Hasselquist, which is closely related to the fig-wasp, and has a similar mode of life. The females do not leave the ripe fruit through the ostium, but through several holes which they make near it.

<sup>1</sup> See Bibliographical Index for a list of papers relating to *Caprification*.

Both females and males are wingless, and the males are distinguished by having a pair of long appendages at the side of the abdomen, which are attached to the stigmata, and probably protect them from the brown sticky pulp within the fruit (466).

Paul Mayer has investigated the wasps of numerous other old world species of figs, mostly from herbarium specimens. In some species of *Ficus* and *Sycomorus* he has found *Blasophaga* and *Sycophaga* together, but the whole number of species of wasps was very small. On the other hand, the Brazilian figs, of which Fritz Müller examined ten species in his own neighbourhood (Blumenau, province of St. Catharina), possess an astonishing variety of wasps belonging to the same family of the *Apocidæ*, some of these belong to the genus *Blasophaga*, some to a genus like *Ichneumon*. Many are adorned with metallic colours, a fact suggests a longer stay in the open air. In point of fact, most of the figs which Fritz Müller studied, flower only once a year, so that many of these wasps must, in order to lay their eggs, visit another tree of the same species which is just beginning to flower at the time when the figs are ripe upon the tree where they themselves were developed. In the case of many species of trees, in fact, at least four migrations are necessary in the course of the year.

In these figs, the old inflorescence from which the male flowers bears only male flowers, and the young inflorescence from which the enter bears only female flowers. Self-fertilization is thus rendered impossible, and separate individuals are regularly produced. The fruit becomes sweet and in many cases gaily coloured when the seeds ripen, and parrots which feed on it help to disperse the seeds (466).

#### GENUS JUGLANS, L.

*Juglans regia* L. is the best suited to the climate of the British Isles. *J. regia*, L. In Europe a sometimes a proterogynous and sometimes a protogynous. (Barrow, *Geobot.* 2.)

#### GENUS CORYLUS, L.

The plants of this genus are not so common in the British Isles as those of the genus *Juglans*, and are excluded from cultivation by the cold winds and frosty weather. I have seen only one specimen of *Corylus avellana* L. in the garden of the University of Cambridge. In many places, however, the hazel *Corylus avellana* L. is common.

ORD. *SALICINÆ*.

378 *a*. *SALIX CINEREA*, L.; 378 *b*. *S. CAPREA*, L.; 378 *c*. *S. AURITA*, L., etc.—In spite of the simplicity of their flowers, which differ little from the anemophilous flowers of the poplar, willows possess special modifications which bring them greater variety of insect-visitors in the first sunny days of spring, and insure them abundant cross-fertilisation. These are: 1, the union of many flowers on one inflorescence, which is not only more conspicuous, but more easily and quickly sucked than so many single flowers; as in all other diclinous entomophilous plants, the male flowers are more conspicuous than the female ones, owing in this case to the bright yellow colour of the anthers; 2, the development of the flowers in many *Salices* before the leaves, which renders the flowers conspicuous among the bare twigs in spite of their want of coloured envelopes; 3, the large store of honey and pollen; and 4, above all, the early period of flowering, which leads many bees, especially many species of *Andrena*, to resort almost exclusively to willows in search of food for their young. These characters, of which the only one probably that has been developed in direct reference to insect-visits is the secretion of honey, have so far insured cross-fertilisation that the plants can well afford to dispense with the power of self-fertilisation. Most diclinic entomophilous flowers (*Asparagus*, *Ribes nigrum*, *Lychnis vespertina*, etc.) seem to have become diclinic by degeneration of their formerly hermaphrodite flowers, but *Salix* seems to inherit its diclinic condition from the oldest phanerogams, which were diclinic and anemophilous.

Visitors: A. Hymenoptera—(a) *Apidæ*: (1) *Apis mellifica*, L. ♀, s. and c.p., very ab.; (2) *Bombus fragrans* (Pall.), K. ♀; (3) *B. hortorum*, L. ♀; (4) *B. lapidarius*, L. ♀; (5) *B. pratorum*, L. ♀; (6) *B. Scrimshirani*, K. ♀; (7) *B. terrestris*, L. ♀, Nos. 2—7 s.; (8) *Osmia rufa*, L. ♂, s.; (9) *Nomada succincta*, Pz. ♀ ♂, very ab.; (10) *N. lineola*, Pz. ♂; (11) *N. varia*, Pz. ♂, ab.; (12) *N. Lathburiana*, K. ♀ ♂, ab.; (13) *N. ruficornis*, L. ♀ ♂, very ab.; (14) *N. signata*, Jur.; all the species of *Nomada* s.; (15) *Colletes cunicularia*, L. ♀ ♂, c.p. and s., in hundreds; (16) *Andrena albicans*, K. ♀ ♂, very ab.; (17) *A. albicus*, K. ♀ ♂; (18) *A. apicata*, Sm. ♀; (19) *A. argentata*, Sm. (= *gracilis*, Schenck) ♀, scarce, ab.; (20) *A. atriceps*, K. (= *tibialis*, K.) ♀ ♂; (21) *A. chrysosceles*, K. ♂; (22) *A. cineraria*, L. ♀ ♂, ab.; (23) *A. Collinsonana*, K. ♀; (24) *A. connectens*, K. ♀, scarce; (25) *A. dorsata*, K. ♀ ♂, ab.; (26) *A. eximia*, Sm. ♂; (27) *A. Flessæ*, Pz. ♀, rare; (28) *A. fulvicrus*, K. ♀ ♂, ab.; (29) *A. Gwynana*, K. ♀ ♂, ab.; (30) *A. helvola*, L. ♀ ♂; (31) *A. nana*, K. ♀ ♂; (32) *A. nigroænea*, K. ♀ ♂; (33) *A. nitida*, Fourc. ♂; (34) *A. parvula*, K. ♂; (35) *A. pilipes*, F. ♂; (36) *A. pratensis*, Nyl. (= *ovina*, Kl.) ♀ ♂, ab.;

(37) *A. punctulata*, Schenk, ♀ ♂; (38) *A. roseæ*, Pz. ♀; (39) *A. Schrankella*, Nyl. ♀; (40) *A. Smithella*, K., ♂, very ab., ♀, scarcer; (41) *A. Trimmerana*, K. ♀; (42) *A. varians*, Rossi, ♀; (43) *A. ventralis*, Imh., ♂, very ab., ♀ scarce: the ♂ of all the *Andrenæ* s., the ♀ s. and c.p.; (44) *Halictus cylindricus*, F. ♀; (45) *H. albipes*, F. ♀, both s.; (46) *Sphæcodes gibbus*, L. ♀, and its varieties, s.; (b) *Vespidae*: (47) *Vespa germanica*, L. ♀, s.; (48) *Odynerus parietum*, L. ♀, s.; (c) *Ichneumonidae*: (49) Various sp.; (d) *Pteromalidae*: (50) *Perilampus* sp., freq.; (e) *Tenthredinidae*: (51) *Dolerus madidus*, Kl., s.; (52) *D. eglanteriæ*, F., s.; (53) *D. gonager*, Kl., s.; (54) *Nematus rufescens*, H., s. R. Diptera—(a) *Empidæ*: (55) *Rhamphomyia sulcata*, Fallen, s.; (56) *Empis* sp., ab., s.; (b) *Bombyliidae*: (57) *Bombylius major*, L., s.; (c) *Syrphidae*: (58) *Eristalis tenax*, L.; (59) *E. arbustorum*, L.; (60) *E. intricarius*, L.; (61)

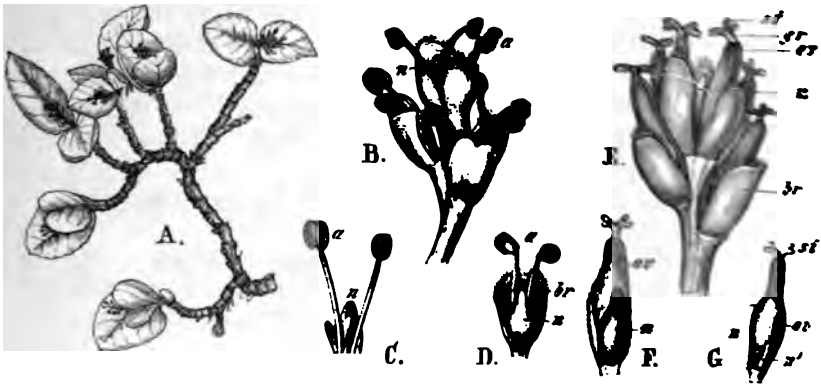


FIG. 177.—*Salix herbacea*, L.

- A.—Part of a male plant (nat. size).  
 B.—Male catkin, with five flowers.  
 C.—Male flower, after removal of the bract, seen from without.  
 D.—Male flower, from within.  
 E.—Female catkin, with six flowers.  
 F.—Single female flower, from within.  
 G.—Ditto, after removal of the bract, seen obliquely from without, so that the large nectary (n) is visible. n', small nectary.  
 (B—G,  $\times 7$ ; Albulæ, 21, 22, July, 1878).

*E. pertinax*, Scop.; (62) *Brachypalpus valgus*, Pz.; (63) *Syrphus pyrastris*, L.; (64) *S. ribesii*, L.; (65) *S. balteatus*, Deg.; (66) *Cheilosia chloris*, Mgn.; (67) *Ch. brachysoma*, Egg.; (68) *Ch. modesta*, Egg.; (69) *Ch. pictipennis*, Egg.; (70) *Ch. præcox*, Zett.; (71) *Syrphia pipiens*, L.; all these *Syrphidae* both s. and f.p.: (d) *Muscidae*: (72) *Pollenia rudis*, F., f.p.; (73) *Calliphora erythrocephala*, Mgn., s.; (74) *Scatophaga stercoraria*, L.; (75) *Sc. meridaria*, I both ab., s.; (e) *Conopidae*: (76) *Sicus ferrugineus*, L.; (77) *Myopa buccæ*, L.; (78) *M. testacea*, L., all three rather freq., s.; (f) *Bibionidae*: (79) *B. Marci*, L.; (80) *B. Johannis*, L., both species s. C. Coleoptera—(a) *Idulidae*: (81) *Meligethes*, ab., l.h.; (b) *Elateridae*: (82) *Limoniæ parva*, Pz. D. Lepidoptera—(a) *Rhopalocera*: (83) *Vanessa urticae*, L., ab., s.; (84) *Lycæna argiolus*, L., s.; (b) *Microlepidoptera*: (85) *Adela* sp., ab. ptera—(86) *Anthocoris* sp., s. See also No. 599, II.

379. *SALIX REPENS*, L.—On the much less conspicuous flowers of this small species, I found only—

A. Hymenoptera—(a) *Apidae*: (1) *Apis mellifica*, L. ♀, s., ab.; (2) *Bombus terrestris*, L. ♀, c.p.; (3) *Andrena ventralis*, Imh., ♀, c.p., ♂, s.; (4) *A. pratensis*, Nyl. ♀, c.p.; (5) *A. albicans*, K. ♀, c.p.; (6) *A. Gwynana*, K. ♀, c.p.; (b) *Tenthredinidae*: (7) *Dolerus eglanteriae*, F., s. B. Diptera—(8) *Bombylius major*, L., s.; (9) *Myopa buccata*, L., s. C. Lepidoptera—(10) *Vanessa Io*, L., s.

*Salix herbacea*, L.—Even this, the smallest of our *Salices*, which straggles over the bare rock of the highest Alps, attracts sufficient insect-visits to be able to dispense with the possibility of spontaneous self-fertilisation; the latter is rendered impossible by the diœcism of the flowers. This fact is strikingly opposed to the common statement that on the Alps (owing to the great scarcity of insects) only those plants which possess the largest and brightest flowers succeed in being fertilised by the aid of insects. The flowers are inconspicuous, but the honey is very abundant. The only visitors that I have found on the flowers of *S. herbacea* are a small moth (*Tineidæ*) and a fly (*Cœnosia* sp.), both sucking honey (609).<sup>1</sup>

#### ORD. EMPETRACEÆ.

*Empetrum nigrum*, L., is anemophilous (762).

#### Gymnospermeæ.

These lowest and oldest Phanerogams have diclinic anemophilous flowers; the female flowers are devoid of a stigma, and possess a cavity in the ovule between the micropyle and the nucleus. In the flowering period, a drop of fluid rests upon the micropyle; the pollen-grains brought by the wind are caught by it, and are drawn within the micropyle as the fluid evaporates or is absorbed (178 I.; 712).

Delpino has given a fuller account of the process of pollination in *Pinus pinaster*, Ait., and *P. halepensis*, Ait., (178) and in *Larix* (177).

#### Monocotyledons.

##### ORD. HYDROCHARIDEÆ.

*Vallisneria spiralis*, L.—The male flowers are set free from the plant and float on the surface of the water. The pollen, which had

<sup>1</sup> Insect-visitors of *Salix fragilis*, L., and *S. amygdalina*, L., are enumerated in No. 590, II.; and those of *S. reticulata*, L., and *S. retusa*, L., in No. 609.

hitherto been protected from contact with the water, is now carried by currents to the stigmas of female flowers. *Vallisneria* is, in a certain sense, a transition from the water-fertilised to the insect-fertilised flowers; *Hydrocharis* is distinctly entomophilous (178, II.).

#### ORD. ORCHIDÆÆ.

This family is remarkable for the following characters, due to its wide distribution and to its enormous number of species: first, for great variety of habit and diversity of station; secondly, for its immense variety of peculiar and highly-specialised flowers; and thirdly, for the unusually large number of seeds produced in each capsule. The diversity of habit and place of growth must be explained by supposing all the parts of the plant concerned in nutrition to have been very variable. I have discussed at full length their variability in our recent species, in a paper upon the genetic relations of *Epipactis viridifolia*, *E. microphylla*, and *E. latifolia* (565).

The multiplicity of forms of flowers is not difficult to understand if we only suppose the ancestors of the family to have been as liable to variation in their flowers as our recent species are. Dr. Rossbach has discussed the variability of the flower in *Orchis fusca*,<sup>1</sup> and I myself in the genus *Habenaria*.<sup>2</sup>

I do not doubt that Orchids owe their extraordinarily perfect adaptations to particular insects not only to the tendency of the parts of their flowers to variation, but also to the separation in time of the two stages in the act of impregnation. At the time of flowering the ovule is, as a rule, not yet developed; pollen is applied to the stigma, and the pollen-tubes grow out, but the ovule is only developed and impregnated weeks or months, sometimes six months, later. The extremely complete adaptations to cross-fertilisation have in their turn resulted, in many cases, in the flowers becoming absolutely sterile to their own pollen.

In regard to capacity for fertilisation by their own pollen, Orchids show the greatest possible differences, all of which, however, are linked together by intermediate conditions. We find in this order, cleistogamic flowers<sup>3</sup> and open flowers; flowers regularly<sup>4</sup>

<sup>1</sup> *Verh. des naturh. Vereins für pr. Rheinl. und Westfal.* p. 166, 1857.

<sup>2</sup> *Ibid.*, pp. 36-47, 1868.

<sup>3</sup> *Schomburgkia*, *Cattleya*, and *Epidendrum* (Crüger, 149); *Dendrobium* (Anderson, 5); *Thelymitra* (Darwin, 167).

<sup>4</sup> *Ophrys apifera* (Darwin, 155); *Neotinea intacta* (Darwin, 159); *Gymnadenia tridentata* and *Platanthera hyperborea* (Asa Gray, 274); *Epipactis viridifolia* (H. Müller, 565); *Epidendrum* (Fritz Müller, 553).

or occasionally<sup>1</sup> self-fertilised; others never self-fertilised, though quite fertile to their own pollen if it be applied artificially (565); flowers absolutely sterile to their own pollen, though fertile not only to the pollen of their own species but even to that of other species of their own genus (158A, 693); finally species in which pollinia and stigma of the same individual act as fatal poisons to one another.<sup>2</sup>

In regard to the immense number of seeds sometimes produced, it may suffice to record an observation of my brother's, who estimated over 1,750,000 seeds in a single capsule of a *Maxillaria* (159).

Dissemination by wind is favoured by the lightness of the seeds and by the peculiar dehiscence of the capsule, which opens by three longitudinal slits, the parts remaining connected above or below.

The subject of the cross- and self-fertilisation of Orchids has been so fully treated in Darwin's classical book and elsewhere that I may confine myself to notes on those of our native species whose visitors have been actually observed, and to some recent additions to our knowledge.

#### Tribes *Epidendreæ*<sup>3</sup> and *Vandæ*.

*Angræcum sesquipedale*, Pet. Th.—This plant is a native of Madagascar. The spur is longer than that of any other Orchid, perhaps than that of any other plant, and according to Darwin (155A, p. 198) an insect must have a tongue 10 or 11 inches long to reach the honey. Mr. W. A. Forbes has given evidence of the existence of such an insect (256). My brother caught a hawkmoth (*Macrosilia Cluentius*) in Brazil which actually had a proboscis 10 or 11 inches long. I have figured this proboscis in No. 571.

In *Notylia*, some species of *Oncidium*, and others, honey is secreted by the outer surface of the ovary and by the bracts. In a *Cattleya* it is secreted for a long period by the young fruit; this honey is diligently sought by ants, but of course has no relation to the process of fertilisation (Fritz Müller).

*Gomeza*.—My brother observed this orchid fertilised by a bee, and saw the fertilised flower produce its capsule.

*Polystachya*.—In a small Brazilian species of this genus, the

<sup>1</sup> *Neottia nidus-avis* frequently, *Listera ovata* exceptionally (Darwin, 159).

<sup>2</sup> Species of *Oncidium*, *Notylia*, *Gomeza*, *Stigmatostalix*, and *Burlingtonia* (Fritz Müller, 550; Darwin, 158A, II. chap. xvii.)

<sup>3</sup> See also No. 34 (*Liparis Bowkeri*), and No. 609, p. 77, fig. 21 (*Corallorhiza innata*).

labellum becomes full of loose cells, like flour, which probably attract insect-visitors (Fritz Müller).

*Epidendrum*.—In South Brazil there are several plain green species of this genus, quite without perceptible perfume, which secrete abundant honey, and must be fertilised by insects. This is an illustration of how flowers need not make themselves perceptible at a distance to their visitors by means which affect our senses.

An observation of my brother's in the island of St. Catharina in South Brazil shows how a plant may propagate itself by self-fertilisation when deprived of the insects for which its flowers were adapted. On this island an *Epidendrum* occurs, whose flower contains three perfect anthers; the two lateral anthers effect self-fertilisation regularly, while the pollen of the third can only be removed by insects, an event which seems to be exceedingly rare. The flower is almost scentless. At Itajahy an *Epidendrum* occurs which resembles the triandrous *Epidendrum* of St. Catharina almost exactly, save that it is monandrous and has a strong, aromatic scent. The triandrous variety can only be looked upon as descended from specimens of the monandrous form which got transported to St. Catharina. There the insects adapted for the flower must have been absent or very scarce, so that the power to reproduce by self-fertilisation became desirable. Accordingly, whenever the two lateral stamens appeared as an abnormality (as often happens in other Orchids) they had the greatest possible chance of being perpetuated by Natural Selection; the perfume of the flowers, on the other hand, being useless and therefore removed from the influence of Natural Selection, was lost (533).

#### Tribe *Neottieæ*.

*Spiranthes autumnalis*, Rich., has been observed by Darwin to be fertilised by humble-bees (155A, p. 127).

380. *LISTERA OVATA*, R. Br.—Sprengel has described the fertilisation of this flower as he observed it in his garden, but he was not acquainted with the insect-visitors. Darwin has given an admirable description of the flower, and mentions two Hymenoptera (*Hæmitiles* and *Cryptus*) which he saw attaching the pollinia to their foreheads; as he caught the insects, he did not witness the placing of the pollinia on the stigma. My own observations may help to confirm and complete the accounts given by Sprengel and Darwin.

On a sunny afternoon in May, 1867, I watched the insect-visitors

of this plant for more than an hour. I was able to watch about twenty plants simultaneously, and on each three or more insects were often busy sucking honey together. I concentrated my attention in every case on a single insect, and did not catch it until it had accomplished at least one act of fertilisation; most of them I only caught after they had fertilised three, four, or more flowers. The specimen of *Grammoptera lœvis* which I have figured (4, Fig. 178) was already laden with pollinia when I first noticed it; it visited six flowers in my presence, carrying off the pollinia from four, and applying pollen to the stigmas of the other two, which had been



FIG. 178.—*Listera ovata*, R. Br.

- 1.—Portion of an unfertilised flower, from the side.
- 2.—Front view of flower, after the pollen masses (po) have been removed from the anther. The flat rostellum (r) is bent forwards, and partly conceals the stigma (st). (Magnified one half as much as 1.) n, nectary.
- 3.—Pollen-masses adhering to a needle ( $\times 20$ ). k, cement; po, pollen-masses.
- 4.—*Grammoptera lœvis*, with a number of pollen-masses on its head.

previously visited and deprived of their pollinia. To judge from the number of hardened cement-disks which this insect carried upon its head, it must have fertilised very many flowers before I began to watch it. Although a great many insects flew away before I tried to catch them, and others escaped me, I secured a considerable number, all of which I had seen effecting cross-fertilisation, and all of which still bore pollinia on their heads. Except *Grammoptera lœvis*<sup>1</sup> they were all Ichneumonidæ. They have been identified for me by Dr. Kaltenbach of Aachen as follows: (1) *Ichneumon uniguttatus* (one specimen); (2) *Alysia* (one); (3)

<sup>1</sup> Sprengel seems to have caught this insect bearing pollinia of *Listera ovata*. At least he mentions a small beetle with black head and scutellum, and brown elytra.

*Cryptus* (eight specimens belonging to three species); (4) *Phagedon* (two); (5) *Tryphon* (two); (6) *Campoplex* (one); (7) *Microgaster rufipes*, F. (three). I saw *Bombus agrorum*, F., licking the honey in several flowers without removing the pollinia.

Sprengel has correctly described how small insects (all of the above, except *Bombus*) regularly alight on the lower end of the labellum ( $p'$ , 2) and slowly creep upwards licking the honey in the groove ( $n$ ); when they have finished and raise their heads, they come in contact without fail with the slightly prominent edge of the thin rostellum ( $r$ , 1). On the slightest touch, this exudes a small white drop of fluid, which reaches the apex of the pollinia ( $po$ , 1) and hardening instantly, cements them to the object whose touch caused the exudation; and so in every flower which has not previously been visited, the insect-visitor receives a new pair of pollinia. The insect flies away startled, and soon afterwards alights on the labellum of another flower, usually on another plant. The rostellum, on first being touched and while it exudes its drop of fluid, curves downwards so as partly to protect the stigma (2, Fig. 178); but afterwards, while the groove of the labellum is secreting a fresh supply of honey, the rostellum gradually rises, leaving the way free to the stigma.

Thus to previous accounts of this flower we may add two statements: 1, that when an insect has once attached pollinia to its head, it must either acquire a new pair of pollinia or apply some pollen to the stigma in every flower that it visits subsequently; 2, that not only does cross-fertilisation always occur, but that the pollen of one plant is usually carried to a flower upon another.

381. *NEOTTIA NIDUS-AVIS*, Rich.—The flower resembles that of *Listera ovata* in regard to the function of the rostellum and its position in relation to the anther and stigma. It differs, however, by concealing its honey from view though leaving it easily accessible, by cementing its pollinia to the insect-visitors in a more irregular and less effective way, and by being frequently self-fertilised owing to the dry pollen falling bit by bit upon the stigma. All such insect-visitors as are attracted only by exposed honey are absent, and the dull yellow flowers deter all those which are only allured by bright colours.

This tendency to self-fertilisation seems to me to be due rather to the mechanism of the flower being as yet incomplete than to scarcity of insect-visits. I have only once watched this plant at

the proper season, but on that occasion I found it visited by flies in considerable abundance, and several of the spikes were covered with spiders' webs. I saw several specimens of *Spilogaster cinerea*, Wied., and a small species of *Muscidæ* alight on the labellum and suck the honey; but I did not see any of them touch the rostellum and remove the pollinia. After watching for a long time, I saw a larger yellow fly (*Helomyza affinis*, Mgn.) visit a flower; when it crawled up the labellum to its base, licking the honey on its way, it came in contact with the rostellum and cemented the pollinia to the anterior part of its thorax. It flew away, startled; but it was caught in a spider's web, and my chance of observing the fertilisation of *Neottia* was lost.



FIG. 179.—*Neottia nidus-avis*, Rich.

- 1.—Lateral view of flower.  
 2.—Ditto, of labellum.  
 3.—Labellum, from above. The small rings indicate honey-drops.  
 4.—Essential organs, in side-view.  
 br, bract; co, column. Other letters as in Fig. 180.

*Goodyera repens*, R. Br.—Mr. R. B. Thomson saw this plant fertilised in the north of Scotland by *Bombus pratorum* (Darwin, 159, 165); I have seen it on the Alps fertilised by *B. mastrucatus*, ♀ (609).

The Alpine *Chamaorchis* is probably adapted, like *Listera*, for fertilisation by *Ichneumonidæ* (609).

*Epipactis latifolia*, Swartz.—Charles Darwin observed this plant to be fertilised by wasps (*Vespa silvestris*). Self-fertilisation seems scarcely possible.

*Epipactis microphylla*, Ehrh., fertilises itself regularly; but part of the pollen can be removed by insects by the aid of the sticky secretion of the rostellum, as the whole pollinia are in *E. latifolia*.

*Epipactis viridiflora*, Rchb., has quite lost its rostellum. Small

portions of pollen may be accidentally carried away by minute insects, but the flower is self-fertilised in a still more conspicuous degree than *E. microphylla*. I have described elsewhere (565) the changes in the relative position of anther and stigma which render self-fertilisation possible, and the intermediate stages between the above-mentioned species of *Epipactis*.

*Epipactis palustris*, Crantz.—Mr. W. E. Darwin saw this species visited and fertilised abundantly in the Isle of Wight by *Apis mellifica*, ♀; also by flies (*Sarcophaga carnosa* and *Cælopa frigida*) and by *Crabro brevis*.

*Epipogon Gmelini*, Rich.—Paul Rohrbach<sup>1</sup> has described the structure and fertilisation of this flower very admirably (675). He observed *Bombus lucorum*, L., visiting the flowers.

#### Tribe *Ophrydeæ*.

*Scrapias longipetala*, Pollin., is visited by bees in the west of Liguria (Delpino, 567).

*Hermidium Monorchis*, R. Br.—George Darwin observed the flowers visited by twenty-seven species of small insects, of which the largest were one-twentieth of an inch long. They consisted of Hymenoptera (especially *Tetrastichus diaphanthus* and *Pteromalini*), Diptera, and Coleoptera (e.g. *Malthodes brevicollis*). I have found the flowers visited on the Alps by small Braconidæ and Pteromalidæ (609).

*Platanthera*.—I have elsewhere (565) proved at very considerable length that the varieties distinguished as *P. bifolia* and *P. chlorantha* by German botanists are connected with one another by numerous intermediate forms; but that the plant referred to by Darwin as *P. bifolia* corresponds to *P. solstitialis*, Bönningh., and is a well-defined species. The spur of *P. solstitialis* is from 12 to 21 mm. long, that of *P. chlorantha* from 23 to 43 mm.; in both species the spur is too narrow to admit a bee's proboscis. The honey is therefore accessible only to Lepidoptera, and in the extreme forms of *P. chlorantha* only to *Sphingidæ*. The colour of the flowers suggests that they are adapted for nocturnal and crepuscular insects. Darwin caught a specimen of *Hadena dentina* to one of whose eyes a sticky disk of *P. chlorantha* was attached, and a *Plusia* with one attached to the margin of its eye. The sticky disks stand much closer together in *P. solstitialis*, and

<sup>1</sup> This able and brilliant naturalist died at an early age.

*Gymnadenia conopsea*, R. Br.—The honey is only accessible to Lepidoptera; the flower to be visited by nocturnal *P. gamma*, *Anaitis plagiata*, *Triphaena*. I have seen this species visited by two of Lepidoptera, mostly butterflies (60).

*Gymnadenia odoratissima*, Rich., (4 or 5 mm., against 13 or 14 mm. in *N. angustifolia*) and stronger and more aromatic perfume. Visited by three species of nocturnal Lepidoptera.

*Nigritella angustifolia*, Rich.—The position of the parts of the flower is, the same as in *Gymnadenia*. Its strong odour of vanilla attracts Lepidoptera (I observed forty-eight species) whose proboscis the pollinia get cemented to.

*Nigritella suaveolens*, Koch., seems to be like *angustifolia* and *Gymnadenia odoratissima*. It cements its pollinia to the upper side of the corolla. In *N. angustifolia* to the lower, it is difficult to be produced, except from flowers of an abnormally inclined. Such abnormality is to be met with now and then in both.

*Anacamptis pyramidalis*, Rich.—It agrees in points with the species of *Orchis* to be like them secretes no free honey. It admits the tongues of Lepidoptera,

and under favourable conditions is covered with a number of minute drops. A *Sarcophaga* which I saw seated on the under lip, licking these drops, flew away on my approach. But it had its head pointing towards the base of the lip, and if I had not disturbed it, it would probably not have failed to lick also the two black shining bodies at the base of the lip; in doing so it would have touched the rostellum and caused a pollinium to be cemented to its head. The two bodies at the base of the under lip look like drops of fluid, though in reality they are quite dry. They may be called *pseudo-nectaries*, and probably deceive the insect-visitors (589, 590, I.).

382-385. ORCHIS MASCULA, O. MORIO, O. LATIFOLIA, and O. MACULATA.—In all these Orchids the three sepals and the two superior petals arch over the essential organs of the flower, while the inferior petal or labellum forms a convenient alighting-place for insect-visitors. The labellum is prolonged backwards into a hollow spur, which secretes no free honey, but whose walls are composed of very delicate and succulent tissue. Immediately above the entrance to this spur stands the trilobed stigma, whose two inferior lobes form the true stigmatic surfaces, while the third superior lobe forms the *rostellum*. This organ, the *bursicula* of German authors, consists of a little pouch full of viscid matter, which projects into the mouth of the spur. The two lateral anthers are just visible as useless rudiments (staminodes); the third, and only perfect one, stands immediately above the rostellum. Its two loculi are separated by a broad connective, and are split anteriorly for their whole length by a longitudinal slit. The two pollinia lie within the loculi, quite unattached except at the ends of their caudicles, which adhere to the upper surface of the rostellum. When an insect thrusts its head into the spur, it inevitably comes in contact with the rostellum; the membrane covering the latter instantly splits into an inferior portion, which curls backwards, and two small round disks, connected with the caudicles and coated abundantly with viscid matter on their lower surfaces; these attach themselves to the insect's head. The cement of the sticky disks quickly hardens, and when, after a short time, the insect withdraws its head, it takes with it the disks and the pollinia attached to them by their caudicles. At first the pollinia stand almost perpendicular to the disks, but soon, as the disks dry, the pollinia bend gradually forwards through an angle of nearly 90°, and so come into such a position that in subsequently-visited

flowers, they are applied directly to the stigma. Each pollinium consists of a great number of packets of coherent pollen-grains; the packets are bound together by delicate elastic filaments to form an oval pollen-mass. When this is pressed against the very adhesive stigma and again withdrawn, all the packets that have come in immediate contact with the stigmatic surface remain adhering to it, for the elastic filaments break before the attachment of the packets to the stigma gives way. By this means, an insect flying from flower to flower effects cross-fertilisation regularly.

This view of the flower of *Orchis* was propounded by Darwin before he or any one else had succeeded in observing insects engaged in the work. Every detail in the structure of the flower seemed to be satisfactorily explained, but the absence of honey in the spur remained without explanation. Sprengel, who supposed that the pollinia were applied by insects to the stigma of the same flower (702, p. 401), suggested that the insect-visitor came in search of honey, and on finding none, passed on to some other kind of flower. But it was essential for Darwin's theory that each insect-visitor should visit a number of the flowers in succession; and Darwin suggested that possibly the insects pierced the delicate tissue of the spur and sucked the included fluid. My own direct observations have confirmed this view, as well as every detail of the rest of Darwin's account. The following description of the action of insects on *Orchis* was published many years ago (565):—

On May 6, 1869, I and my son Hermann at length succeeded in observing humble-bees fertilising the flowers of *Orchis* upon Stromberg Hill. As we lay upon the turf, which was overgrown with *Orchis mascula*, we saw a humble-bee (apparently *Bombus terrestris*) alight, close beside us, on the base of a spike of that plant. It thrust its head into a flower, and drew it out after about four seconds with the two pollinia attached to it. It repeated the same operation on two more flowers. After withdrawing its head from the third, it paused, and tried without success to free itself from the pollinia, which were cemented firmly to the front of its head. Climbing a little further up the spike it thrust its head into a fourth flower. At that moment I tried to catch it in my net, but it escaped and flew away. We next saw a *Bombus hortorum* suck three or four flowers on a spike of *Orchis mascula* (beginning at the base of the spike), and then proceed to another spike, near by. We examined this latter spike, and found several of its stigmas smeared with pollen and the loculi of

the anthers empty. In the space of two hours we had three more opportunities of watching the fertilisation of *Orchis mascula*; the fertilising agent on two of these occasions was *Bombus lapidarius*, on the third, *Psithyrus campestris*. *B. lapidarius* spent a shorter time on each flower (about two to three seconds), but otherwise the various bees behaved precisely alike. We caught the *Psithyrus* and a *B. lapidarius*, and found a number of pollinia on the head of each. Some of the pollinia had already bent forwards, so that they were ready to come in contact with the stigma of the next flower; others were still erect. Of ninety-seven humble-bees which we caught that day on Stromberg Hill, thirty-two bore pollen-masses of *Orchis*. We frequently observed on our captured bees, that when the pollen-masses bent forwards the bee was able to tear them off with its mandibles. Some bees which we caught with pollinia on their heads had them attached to their forelegs when examined shortly afterwards. These frequently successful efforts on the part of the bees to free themselves from the pollinia explain why we often find whole pollinia or pairs of pollinia attached to the flowers, generally in the neighbourhood of the stigma.

On this one day, which was especially favourable, as it was warm and calm, and came after a long spell of cold weather, probably more than a third of all the humble-bees on Stromberg Hill had been engaged in fertilising *Orchids*. The following numbers give a rough idea of the scale on which the work was performed. At seven o'clock on the morning of the same day I gathered ten specimens of *Orchis morio* on a meadow covered with the plant. These ten spikes contained 107 expanded flowers; of these, one only had its anther-loculi empty and its stigma smeared with pollen; two had their stigmas smeared with pollen, but their pollinia had not been removed. At five o'clock in the afternoon I gathered in the same place ten spikes containing ninety-seven flowers; fourteen had their stigmas smeared with pollen, and of these two only had their pollinia still within the anther-loculi; three other flowers had their pollinia removed, but their stigmas showed no trace of pollen. Thus at seven o'clock in the morning 2·5 per cent., and at five o'clock in the afternoon over 14 per cent. of the flowers had been fertilised.

I need hardly add that this observation fully confirmed Darwin's suggestion. The bees must have found something within the spurs, or they would not have continued to visit the flowers. Since the spur contains no free honey, but abundant fluid within its

floor, which are sometimes covered with small drops of honey. They try for some time to escape by climbing up the vaulted sides of their prison towards the orifice that they entered by; at last after creeping beneath the stigma ( $\sigma$ , 2, Fig. 180), they manage with a great effort to escape by one of two small lateral openings ( $ex$ , 2) at the base of the lip; in doing so they smear one shoulder with a sticky pollen from the anther immediately above. In the

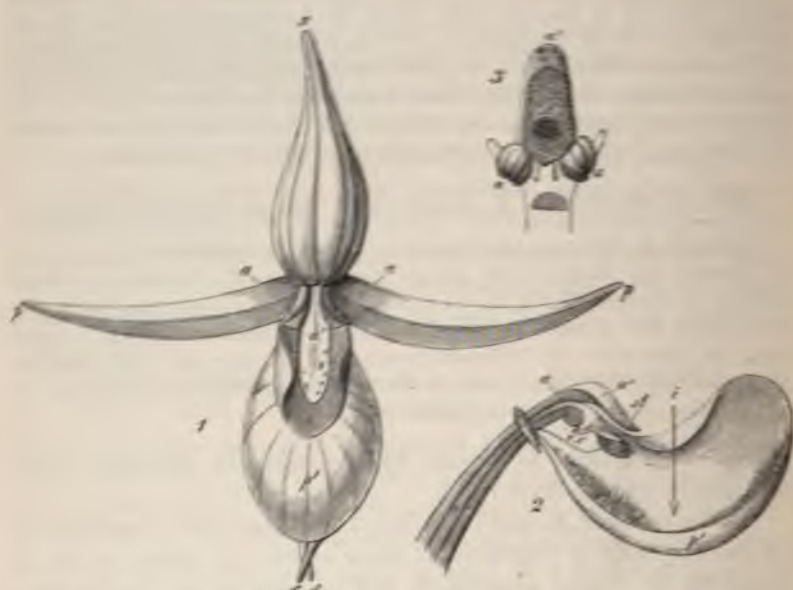


FIG. 180.—*Cypripedium Calceolus*, L.

- 1.—Flower, with its parts in their natural position, seen from in front and above.
- 2.—Ditto, in longitudinal section, after removal of the sepals and the two superior petals. (The lip is bent slightly downwards, to show the opening  $ex$  clearly).
- 3.—The essential organs from below.

$ov$ , ovary;  $s$ , sepal;  $p$ , petal;  $p'$ , labellum;  $a$ , anther;  $a'$ , metamorphosed stamen;  $\sigma$ , stigma;  $i$ , "entrance";  $ex$ , "exit."

next flower, the bee, as it creeps under the stigma, leaves some pollen on its papillæ, which are long and point obliquely forwards; then, squeezing itself again through one of the small orifices, it acquires another load of pollen: cross-fertilisation is thus effected regularly. The third anther ( $a'$ ) is metamorphosed into a broad, purple-spotted lobe, which stands in the posterior half of the cavity of the lip and leaves only the small lateral orifices described above. The hairs, which are arranged in a broad band on the floor of the labellum, seem to help the *Andrenæ* to climb up towards the orifices, besides

attaching them by their secretion. Smaller bees and flies which are too large to pass freely through the orifice and too weak to force their sides apart, must as a rule perish of hunger within the labellum. I have repeatedly found *Andrena parvula*, K. ♀, dead within the labellum, and also the following flies: *Empis punctata*, F., a *Cheilosia* (*Syrphidæ*), an *Anthomyia* (*Muscidæ*), and considerable numbers of *Spilogaster semicinera*, Wied. (*Muscidæ*). Small beetles (*Meligethes*) are often able to creep freely out of the labellum, but sometimes they are held fast by the sticky pollen and remain to perish.

*Cypripedium barbatum* is believed by Delpino to be fertilised by flies. Delpino found flies within the labellum of some cultivated plants, which afterwards set seed (178, 567).

*Cypripedium caudatum* is believed by Delpino to be fertilised by snails (178).

#### THE ADAPTIVE MODIFICATIONS OF ALPINE ORCHIDS COMPARED WITH THOSE OF THE LOWLANDS.

A review of the Orchids that I have observed upon the Alps shows that, above the limit of trees, almost the only species which occur are those adapted for Lepidoptera, while in the lower regions forms adapted for all kinds of visitors occur. The following species occur in greater abundance above the level of trees, or are restricted entirely to that region: (1) *Orchis ustulata*, (2) *O. globosa*, (3) *Gymnadenia conopsea*, (4) *G. odoratissima*, (5) *G. albida*, (6) *Peristylus viridis*, (7) *Nigritella angustifolia* (*N. suaveolens*, as being probably a hybrid, cannot be included), (8) *Platanthera solstitialis*, (9) *Chamaorchis alpina*. Of these, six (1, 2, 3, 4, 7, 8) are undoubtedly, and two (5, 6) (from the narrow entrance to the spur) in all probability, are fertilised by Lepidoptera. While we thus find that of the loftier Alpine Orchids at least two-thirds, but probably eight-ninths, are adapted for Lepidoptera, in Westphalia we find that, of thirty-five species,<sup>1</sup> at most six<sup>2</sup> are adapted for Lepidoptera, and most of these are very sparingly visited by them (609).

<sup>1</sup> *Orchis pyramidalis*, *O. morio*, *O. mascula*, *O. laxiflora*, *O. coriphora*, *O. militaris*, *O. tridentata*, *O. sambucina*, *O. latifolia*, *O. maculata*, *Gymnadenia conopsea*, *G. albida*, *Platanthera bifolia* (*solstitialis*), *P. chlorantha*, *Peristylus viridis*, *Hermidium Monorchis*, *Ophrys muscifera*, *O. apifera*, *O. aranifera*, *Epipogon Gmelini*, *Cephalanthera pallens*, *C. ensifolia*, *C. rubra*, *Epipactis latifolia*, *E. microphylla*, *E. viridiflora*, *E. atrorubens*, *E. palustris*, *Listera ovata*, *Goodyera repens*, *Spiranthes autumnalis*, *Malaxis paludosa*, *Liparis Loeselii*, *Cypripedium Calceolus*.

<sup>2</sup> *Orchis pyramidalis*, *Gymnadenia conopsea*, *G. albida*, *Platanthera bifolia* (*solstitialis*), *P. chlorantha*, *Peristylus viridis*.

## ORD. SCITAMINEÆ.

## Tribe Zingiberæ.

*Hedychium* and *Alpinia* are adapted for cross-fertilisation by insects. The visitors must come in contact first with the stigma and afterwards with the anthers (172, 352). Delpino conjectured that *Hedychium* must be fertilised by Lepidoptera, and long afterwards found scales of Lepidoptera on the stigma of the plant (177). Fritz Müller has shown that the flowers of *Hedychium* are arranged so that the pollen may be transported by the wings of long-tongued butterflies.

*Zingiber officinarum*.—Cross-fertilisation is ensured in case of insect-visits by the prominent position of the stigma (351).

The cultivated plant in South Brazil is only reproduced by vegetative means, and is quite barren, though pollen, stigma, and ovule seem to reach normal development. This sterility is perhaps due to the plants being all portions of one original stock (359).

## Tribe Marantæ.

*Calathea* (*Maranta*) *zebrina*, Meyer, and *C. discolor*, Lindl., have, according to Hildebrand, an explosive arrangement, comparable to that of several Papilionaceæ. A hood-shaped petal, on the under side of the almost horizontal flower, surrounds the style, which carries at its extremity the funnel-shaped stigma, and above the stigma the pollen which is shed upon it in the bud. The weight of an insect-visitor alighting on the petal itself or on a hooked process of it, sets the style free. The style then curves backwards and inwards, so that the ventral surface of the insect is first swept by the stigma and then dusted with fresh pollen. The style in curving backwards closes the path to the honey, so that each flower is only visited once (360, p. 617). Delpino investigated *Maranta bicolor* and *M. cannaefolia*, and found their flower almost identical in structure with the species described by Hildebrand. He, however, found that part of the style between the stigma and the pollen secretes a sticky fluid, which is applied to the insect's proboscis and causes the pollen to adhere.

*Thalia dealbata*, Fras., has similar flowers, which are visited and fertilised abundantly at Florence by the hive-bee.

Delpino has tried, by comparing the flowers of *Marantaceæ* with those of *Musaceæ*, *Zingiberaceæ*, *Cannaceæ*, *Orchideæ* and *Gramineæ*, to trace out the genetic relations of these orders (175).

*Maranta arundinacea*, L., is sterile in South Brazil, where it is only propagated asexually. The flowers have ceased to produce pollen, but retain the elastic style (359).

#### Tribe *Cannæ*.

*Canna*.—At an early period the anthers shed all their pollen upon the expanded style, from which it is removed by insects and conveyed to other flowers (Delpino, 172). According to Hildebrand, spontaneous self-fertilisation very often takes place, and leads to the production of good fruit (351, 352).

#### Tribe *Musæ*.

*Strelitzia reginæ*, Ait.—The two inner and inferior perianth-segments, which inclose the five anthers, separate when a visitor presses upon them in trying to enter the flower; the anthers then emerge and come in contact with the under surface of the visitor. The stigma is exerted, and is accordingly always touched before the anthers. Delpino supposed, and Darwin showed by direct observation, that the fertilisers are honey-sucking birds (356, p. 508; 360, p. 673; 178, p. 232; 567, p. 4). At the Cape of Good Hope, it is fertilised by Nectarinidæ (164, p. 371).

*Musa*.—The Bananas which are cultivated in South Brazil and propagated only by asexual means, are barren; their anthers produce very little pollen and wither without dehiscing (359, p. 275). The flowers of *Musa* attract insects by an abundant secretion of sweetish jelly. *Trigona ruficrus*, Latr., is attracted in swarms (590, I. p. 14).

#### ORD. *IRIDÆ*.

387. *IRIS PSEUD-ACORUS*, L.—The honey is secreted by the lower portion of the perianth (*d d'* 1, Fig. 181), and is collected in the space (*b*) between it and the pistil (*a*). Access to it is only possible at three points, between the lower portion of each outer lobe of the perianth and that of the petaloid style above it. The filament, adhering as a longitudinal ridge to this portion of each perianth-segment, divides the passage to the honey into two separate openings (*b b*); thus altogether six somewhat narrow passages, two at the base of each stigmatic lobe, bounded laterally by the projections from the outer perianth-segments, form the only approaches to the honey. An insect must have a proboscis at least 7 mm.

the petaloid styles and the three anthers. The surfaces are directed downwards. Self-fertilisation is impossible.



FIG. 181.—*Iris Pseud-acorus*.

- 1.—Transverse section through the tubular part of the perianth.
- 2.—Transverse section through the perianth, at the point where the style divisions and the outer segments of the perianth are visible.
- 3.—Transverse section somewhat higher than 2, to show the ridges of the style and the outer segments of the perianth. *a*, style; *a' a' a'*, the three foliaceous divisions of the style; *b*, of filaments, adherent to the outer segments of the perianth, *d*, perianth; *e e*, the two ridges on each outer segment of the perianth; the filaments, bound the entrance to the nectary.

Sprengel,<sup>1</sup> has given a very full account of the flowers of *Iris Pseudacorus* and *I. Xiphium*. Insect-visitors were, however, not near the conception of the mode of fertilisation much.

In Sprengel's opinion, both species of *Iris* are visited by humble-bees. A bee alights on one of the perianth, toward the base of which it is a long, over-hanging petaloid style, until it reaches the nectary. After it has sucked the honey,

petaloid style, which is the functional stigma; a little further on it rubs against the pollen-covered surface of the anther, which lies close to the petaloid style. In this way, Sprengel declared that two stigmas in each flower were regularly fertilised by means of pollen from the previously-visited anthers of the same flower, and that the stigma first visited in each flower was always cross-fertilised by means of pollen from the preceding flower: thus self-fertilisation took place twice as frequently as cross-fertilisation. Though Sprengel was not aware of the advantage of cross-fertilisation, he was repeatedly led by his observations to the conclusion "that nature is unwilling that any hermaphrodite flower be fertilised by means of its own pollen." In order to adhere to this theory in the case of *Iris*, which he abandoned again and again in other cases, Sprengel chose to look upon each third of the flower in *Iris* as a separate hermaphrodite flower, which thus was regularly cross-fertilised.

My frequent observations of insect-visits differ materially from Sprengel's view of the case. It is true that humble-bees visit the flower of *Iris pseudacorus*, but they, as a rule, act in a way very different from that which Sprengel described; and a very much more frequent visitor is, in my experience, the long-tongued hover-fly, *Rhingia rostrata*.

In many flowers of *Iris pseudacorus* the petaloid styles stand 6 to 10 mm. above the corresponding outer perianth-segments. In others each petaloid style lies so close to the perianth-segments that only a very small passage is left, which, owing to the convexity of the style, lies immediately below the stigma. These two forms of flowers have adapted themselves to different fertilising agents.

In flowers of the first variety the fly (*Rhingia*) crawls along the outer perianth-segment to the nectaries without touching either stigma or anther; it inserts its proboscis (11 mm. long) into one nectary after the other, and then moves a few steps backwards to feed on the pollen. When under the anther it raises its head, stretches out its tongue, and so reaches the pollen. Then it flies to another perianth-segment of the same flower, or to another flower. Its visits to this variety are thus not only useless but hurtful, leading to waste of pollen.

In flowers of the other form this fly creeps through the small passage beneath the true stigma, and touches with its back first the stigma and then the anther before reaching the nectaries. After sucking, it creeps backwards without staying to eat pollen, until it

to carry pollen to the stigmatic surface, of flower, and (2) it is hindered from eating the flowers of the other form, *Rhingia* pass accomplishing fertilisation, and moreover as honey.

In relation to bees' visits the condition. When the petaloid style lies close upon segment, the opening, which is sufficient too small to admit a humble-bee. On May a large parasitic humble-bee (*Psithyrus* very long, and 10 mm. broad) creeping in various flowers; finally, placing its head above the an outer perianth-segment, it inserted its tongue of the nectaries, and so reached the honey of the stigma or anther.

In flowers of the other form, I have observed case of *Bombus agrorum*, *B. hortorum*, and other bees alight on one of the outer perianth-segments, the petaloid style to the honey-passages, both stigma and anther with their backs backwards along the path they came by, to one of the other outer perianth-segments to enter beneath the stigma, as before. circuit of the flower and exhausting all its another, and so effects cross-fertilisation results.

Occasionally, but only in those few flowers of the petaloid styles was intermediate between have described as typical, I have seen humble-bees crawl forwards from under cover of the style, as seen in

The flowers of *Iris pseudacorus* thus

Those flowers fitted for fertilisation by bees are at an advantage in that the bees always cause cross-fertilisation of separate plants; but at a disadvantage from having their pollen exposed to robbery by *Rhingia*. The flowers adapted for fertilisation by *Rhingia* have the disadvantage that self-fertilisation is as frequently or even more frequently caused than cross-fertilisation; but possess the advantage that their pollen is not liable to be wasted, and that they receive more numerous visits. Advantages and disadvantages must be about equally balanced in the two varieties, since natural selection has not enabled either to outstrip the other. The rarity of intermediate forms is explained by the fact that such forms combine the disadvantages of both extremes; cross-fertilisation is not secured, and the pollen is not protected from robbery.

Besides the visitors already mentioned one or two useless guests frequent the flowers. On the variety in which the perianth and styles stand wide apart, I once saw *Osmia rufa*, ♀, engaged in sucking honey. This bee was enabled, by the length of its proboscis (8 mm.), to enjoy the honey without touching either stigma or anther. I once saw a hive-bee trying to obtain honey. It crept beneath a style without touching the stigma or anther, as far as the honey-passages, and then stretched out its proboscis (6 mm.), which, however, was too short to reach the honey. After several unsuccessful attempts the bee deserted the plant and settled on flowers of *Ranunculus acris*.

Visitors: A. Hymenoptera—*Apidae*: (1) *Bombus vestalis*, Fourc. ♀; (2) *B. agrorum*, F. ♀ ♂; (3) *B. hortorum*, L. ♀ ♂; (4) *B. Rajellus*, Ill. ♀, all four sucking; (5) *Osmia rufa*, L. ♀, sucking without effecting fertilisation; (6) *Apis mellifica*, L. ♀, vainly sucking honey. B. Diptera—*Syrphidae*: (7) *Rhingia rostrata*, L., s. and f.p.

A species of *Cypella*, in S. Brazil, according to Fritz Müller, increases its conspicuousness very effectually by not expanding its flowers regularly day by day but by concentrating them upon certain days (597).

*Crocus vernus*, All.—Honey is secreted by the ovary, and rises in the narrow tube (almost filled by the style) nearly to the upper, somewhat expanded end. It can only be completely extracted by long-tongued Lepidoptera, while humble-bees as a rule can only skim the surface. By the violet or more frequently white colour the flowers seem to be adapted for crepuscular and nocturnal Lepidoptera. I have found them visited by *Plusia gamma*, less often by *Vanessa cardui*, and occasionally by humble-bees. At first,

self-fertilised, the style curving back.

*Gladiolus segetum* has proteran Labiate type according to Delpin maphrodite flowers others occur p. 184, 360, p. 670).

*Gladiolus palustris*, Gand., and by bees and humble-bees (590, 1).

ORD. LILL.

388. ASPARAGUS OFFICINALIS, undoubted instance of a transition

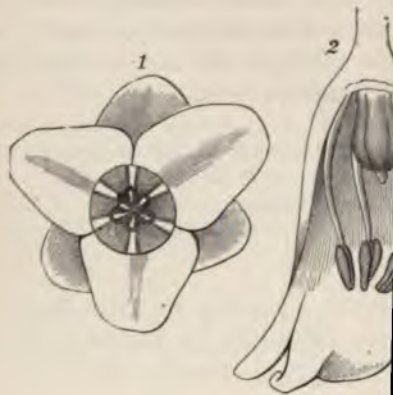


FIG. 182.—*Asparag*

- 1.—Male flower, from bel
- 2.—Ditto, after removal
- 3.—Female flower, from
- 4.—Ditto, after removal
- a, rudimentary stamen ;

anthers (*a*, 3). Occasionally reversion to the hermaphrodite condition takes place, and then in the hermaphrodite flowers the pistil may sometimes be seen in various degrees of abortion.<sup>1</sup> The pendulous bell-shaped flowers have a pleasant scent; in spite of their inconspicuous colour they are easily visible at a distance, the male flowers, which are 6 mm. long, being much more so than the females (3 mm.). This instance confirms Sprengel's oft-repeated rule that the male flowers of diclinic plants are more conspicuous than the female, whence insects are likely to visit the two kinds of flowers in the proper sequence. Honey is secreted and lodged in the base of the corolla.

Visitors: Hymenoptera—*Apidae*: (1) *Apis mellifica*, L. ♀, s. and c.p., very ab.; (2) *Osmia rufa*, L. ♀, s.; (3) *Megachile centuncularis*, L. ♀, s.; (4) *Prosopis annularis*, K. (Sm.) ♀, s.; (5) *Halictus sexnotatus*, K. ♀, c.p., here and there looking for pollen in the female flowers and effecting fertilisation occasionally.

389. *CONVALLARIA MAJALIS*, L.—When the flower opens, and before the anthers ripen, the stigma is already covered with long

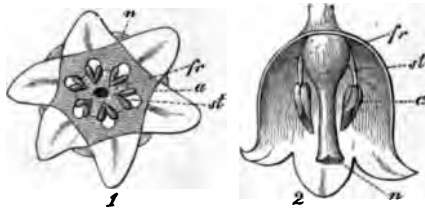


FIG. 183.—*Convallaria majalis*, L.

- 1.—Flower, from below.  
2.—Ditto, after removing half the corolla, with three of the stamens.  
*st*, filaments; *a*, anthers; *fr*, ovary; *n*, stigma.

papillæ; yet if a ripe anther be passed over its surface scarcely any pollen adheres. Afterwards, when the anthers have dehisced, the stigma becomes covered with a sticky fluid, to which pollen adheres readily. I have not found honey in the flowers, though I have frequently seen hive-bees visiting them. The bees collected pollen hanging to the pendulous flowers and inserting their heads and forelegs. They thus brought their heads in contact with the stigma before the anthers, and performed cross-fertilisation regularly. Then as the bee swept the pollen from the anthers with the tarsal brushes of its forelegs, it dusted its head anew

<sup>1</sup> Breitenbach, *Bot. Zeitung*, Nov. 11, 1878.

insects, and the pendulous position of rain. Humble-bees visit the flowers; the wide part of the tube, and touch in the mouth of the flower, and the taneously with it, with opposite sides. They thus effect cross-fertilisation, the bee in touching one side of the tube side against the anthers. In absence of self-fertilisation occurs.

Visitors: A. Hymenoptera—*Apidae*: (1) (2) *B. hortorum*, L. ♀ (19–21), s., hanging at the mouth of the same flower,—sucking in pollen is too short to reach, then collecting pollen by stroking the stigmas.

*Convallaria verticillata*, L., is adapted for fertilisation by *C. polygonatum*, L., for fertilisation by and stigma are matured simultaneously, at least, some pollen as it emerges from the stigma. It is probable that it is pollen brought from other flowers (60).

*Aspidistra elatior*, Blume.—Buchner examined the flower thoroughly, but was unable to explain the mechanism fully. Delpino, however, was successful, to explain the mechanism, he failed to find it visited by insects (61).

The capitate stigma closes the flower openings through which Delpino saw the pollen falls out of the anthers.

*Rohdea japonica*, Kunth.—This plant is, according to Delpino, a link between the *Asparagineæ* and the *Aroideæ*. It possesses a kind of spadix, on which the flowers are arranged in a close, uninterrupted spiral. The fact that the limb of the perianth is spread out exactly on a level with the points of the anthers and stigma led Delpino to think that fertilisation was effected by small animals crawling over the flowers. He observed snails (*Helix aspersa*, *H. vermicularis*) greedily eating the perianth, which is yellow and fleshy; after devouring about ten flowers they crawled to another spadix. Only those flowers on which the snails had crawled proved fertile; the flowers were found to be barren to their own pollen. These observations leave no doubt that snails are really efficient fertilising agents.

*Tritoma Uvaria* is adapted for fertilisation by diurnal Lepidoptera (228).

*Yucca*.—According to Riley (108) the species of *Yucca* which are provided with a dehiscent capsular fruit, and the moth which

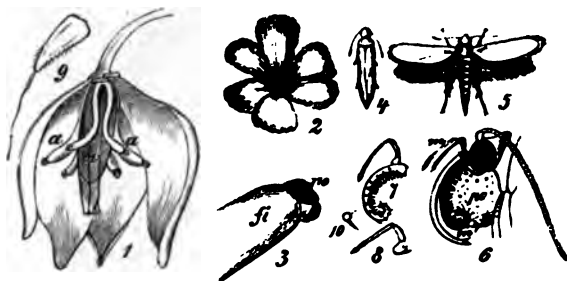


FIG. 184.—*Yucca* and the *Yucca*-moth.

- 1.—Flower of *Yucca recurvata*, Salisb., from Georgia. Two segments of the perianth have been removed to show the ovary (ov) and stamens (a).  $\times 4$ .
  - 2.—Stigma, from above,  $\times 4$ .
  - 3.—End of a stamen,  $\times 4$ . fil, filament; po, pollen.
  - 4.—The *Yucca*-moth, *Pronuba yuccasella*, Riley.
  - 5.—Ditto, with outspread wings.
  - 6.—Head, m, mandibular palps; m', first joint of ditto; po, pollen.
  - 7.—Mandibular palps of female.
  - 8.—Ditto, of male.
  - 9.—Ovipositor.
  - 10.—A bristle from 7.
- (4—10, after Riley).

effects their cross-fertilisation (*Pronuba yuccasella*, Riley) stand in close interdependence. In the female of this moth the first joint of each of the two maxillary palps is transformed into a long prehensile organ, which can be rolled up, and which serves to seize the pollen with. After the female has bored the ovary in several

winter, and spring; it passes into days before the Yuccas begin to flower when they do so (667—671, &c.).

*Paradisica Liliastrum*, Bertolon nocturnal Lepidoptera. The honey is secreted, as in *Convallaria*, by the ovary, between the carpels. The stamens and anthers are placed as in *Lilium*, and many other nocturnal

*Eremurus spectabilis*.—The flowers open before the stigma and anthers are ready. Weigelia, Lantana, and many other flowers gain hereby is that the less insects are attracted away to the more conspicuous treasure for them (612).

391. ANTHERICUM RAMOSUM, L. The flowers open widely, exposing their honey, so that lipped insects can see and reach it. The upper part of the ovary, on which the honey is placed (pl. xxiii. fig. 8).

On the Rehmsberg near Mühlhausen, opportunity of observing this plant in its natural surroundings. The flowers were visited by bees, sucking honey and collecting pollen. They first touched the projecting stigma, thus causing cross-fertilisation regularly. The honey-fly (*Merodon æneus*, Mgn.) hovered in great numbers than the honey-bee, sucking honey. It was in fact the principal fertiliser.

sat upon one flower while sucking another, cross-fertilisation (owing to the prominent situation of the stigma) was often effected by pollen adhering to the under surface of their bodies. In absence of insects, self fertilisation can only take place in flowers directed more or less downwards.

Visitors : A. Hymenoptera—*Apidae* : (1) *Apis mellifica*, L. ♂, s. and f.p. B. Diptera—*Syrphidae* : (2) *Merodon æneus*, Mgn., s. and f.p. C. Lepidoptera—*Rhopalocera* : (3) *Papilio Machaon*, L., s. ; (4) *Melitæa Athalia*, Esp., s. Visited also by many other insects. See No. 590, 1.

*Anthericum Liliago*, L.—The flower resembles that of the former species (590, 1).

392. *ALLIUM URSINUM*, L.—When the flower first opens the style is only from one-third to one-half of its ultimate length ; the papillæ are not yet developed on the stigma, and the anthers are still all immature. First of all the three inner anthers dehisce at slow intervals, one after the other ; at this stage the style has reached three-quarters or more of its full length ( $4\frac{1}{2}$  to 5 mm.). Then the three outer anthers dehisce one after another ; the style has now reached its full length (6 mm.), and the papillæ on the stigma become developed. The flowers are thus imperfectly proterandrous. The anthers dehisce introrsely, and then turn that side which is covered with pollen more or less upwards. In specimens flowering in my room I found some flowers in which the style was so bent during the last stage that the stigma touched one of the anthers which still retained some of its pollen. In this way self-fertilisation was effected to a limited extent when no insect visited the flower. In a wood at Stromberg Schlossberg on the 16th May, 1868, I saw *Bombus pratorum*, ♀, flying quickly from flower to flower of *A. ursinum* ; she thrust her proboscis into each flower in search of honey, and after scarcely two seconds hurried on. The honey is secreted by the ovary, in the three notches between the carpels, and fills the space between these notches and the bases of the three inner stamens. Hence the bee when sucking must touch the stigma with one side of its head and the anthers with the opposite side, and, in old flowers, can only lead to cross-fertilisation.

393. *ALLIUM CEPA*, L.—The honey in this species is placed in the same position as in the preceding one ; the anthers and stigma are also similarly situated.

*Allium Schænoprasum*, *B. alpinu*  
in honey. It is much visited by st  
2,000 m. above the sea-level (665).

*Allium rotundum*, L., is adapted  
and bees. The three nectaries ar  
bases of three of the stamens; the  
the stamens protrude from the flow  
the bee towards the honey (590, 1).

*Allium victorale*, L., is markedl  
displayed openly, and the yellowish  
ceedingly conspicuous on their tall  
flies, bees, and Lepidoptera (609).

*Allium sibiricum* has proterandr  
figured by Axell (17).

The flowers of *Hemerocallis fu*  
pollen according to Sprengel (p. 43)

*Muscari botryoides*, Mill., and *M*  
by bees and adapted for fertilisation

*Scilla maritima*, L., is visited by

394. HYACINTHUS ORIENTALIS,  
tube, 12 to 14 mm. or more in lengt  
and recurved teeth. In its lower t  
style and tripartite stigma; in the  
which dehisce introrsely and ripen a  
No free honey is secreted, but the  
and succulent, and is probably b  
visitors. When an insect's probos  
touches the anthers and stigmas wit

three glands in the angles of the ovary, but I have not been able to detect it (cf. W. J. Behrens, No. 51).

Visitors : A. Hymenoptera—*Apidae* : (1) *Bombus terrestris*, L. ♀ ; (2) *Anthophora pilipes*, F. ♀ ♂, ab. ; (3) *Andrena fulva*, Schr. ♀ ; (4) *Osmia rufa*, L. ♂, very ab., all sucking. B. Diptera—*Syrphidae* : (5) *Cheilosia* sp. sucking in vain for honey. C. Coleoptera—*Nitidulidae* : (6) *Meligethes*, on the anthers in large numbers, apparently feeding on the pollen. See also No. 590, I.

*Lloydia serotina*, Rchb.—This plant shows an advance on the foregoing Liliaceæ in the possession of special nectaries, consisting of a thick ridge at the base and in the middle line of each segment of the perianth. The flower is proterandrous, but the stigma ripens simultaneously with the inner whorl of stamens; in some cases it stands on a level with their anthers, in others above them, so that self-fertilisation is possible or not respectively (609).

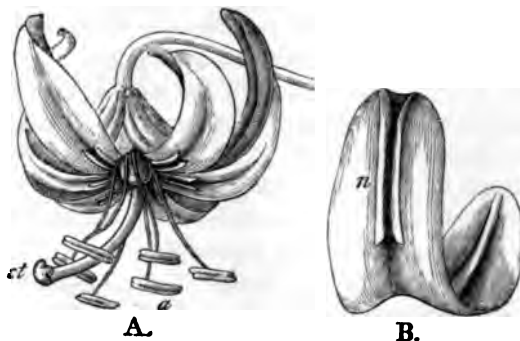


FIG. 185.—*Lilium Martagon*, L.

A.—Flower, in its natural position, seen from the side (natural size).  
B.—A petal ( $\times 2$ ).  
n, entrance into the nectary (n).

*Lilium Martagon*, L., is adapted for cross-fertilisation by Sphingidæ; Noctuidæ also assist in the work. The anthers and stigma ripen simultaneously, and are touched by the feet and under surface of the insect. Self-fertilisation also occurs, as Sprengel found. The perfume of the flower begins to be emitted strongly at night (570, 590, I, 609).

*Lilium bulbiferum*, L., is adapted for fertilisation by diurnal Lepidoptera. A nectary in this species and in *L. Martagon* is situated in the middle line at the base of each segment of the perianth; but it is not a ridge merely, as in *Lloydia*, but a deep groove, whose edges, bordered by stiff hairs, rise up and arch over

395 COLCHICUM  
of a long, tubular  
from the honey wt  
lization. But Spre  
in this plant the len  
from the bulb is n  
buried in the earth.  
to be sheltered from c  
lie in the corolla-tube.  
of the lower part of th  
within grooves of the  
The stigmas mature be  
overlooked, but remain  
anthers ripen. If insec  
is inevitable, owing to th  
if they do not occur till  
it is rendered unlikely by  
their pollen-covered surface  
this movement of the anth  
fertilization.

On the morning of Sep  
flowers still closed in the  
displayed anthers not yet  
pollen. Rather later, wher  
males of *Bombus hortorum* bi  
flower, and sucking

*Tofieldia calyculata*, Wahlenb., is proterogynous; *T. borealis*, Wahlenb., is homogamous. The flowers in both species are yellow, and the visitors are chiefly, but not exclusively, flies and beetles. The much smaller flowers of *T. borealis* are less visited than the more conspicuous flowers of *T. calyculata*, but the former species makes up in part by an increased secretion of honey. Its flowers, being homogamous, have a better chance of self-fertilisation in default of insect-visits (609).

*Methonica (Gloriosa) superba* has a pendulous flower, whose stamens and style are directed horizontally outwards, and serve, according to Delpino, as a platform for insects (172). Hildebrand states that in young flowers the style serves as an alighting-place, while the stamens lie deeper; and that in older flowers the stamens assume this function, so that cross-fertilisation of young flowers with pollen from older proceeds regularly (352).

*Paris quadrifolia*.—I was long puzzled to discover how this flower is fertilised.

The stigmas are already mature when the flowers open; the anthers dehisce several days later, the stigmas still remaining fresh. The pollen-grains are about .04 mm. long by .016 mm. broad; they remain adhering in great quantity to the ripe anthers, but fly off on the slightest touch in a cloud of separate grains. The nature of the pollen and the complete absence of honey and of a coloured perianth point to the flowers as being anemophilous. The stiff filaments and the long connectives, which are produced into awn-like prolongations, do not support this view, unless they assist the transport of the pollen by the wind when they are shaken by pollen-feeding flies alighting on them.

I wrote the above in 1872, and I did not discover till six years later that the flower of *Paris* becomes intelligible in all its parts when one looks upon it as adapted for Diptera; and I observed then that in fact it is visited by Diptera. The dark purple ovary, crowned by four stigmas of the same colour, glitters as if it were covered with moisture; and by this appearance and by its disagreeable smell it attracts *Scatophaga merdaria* and other carrion-feeding Diptera. These visitors often alight upon the stigma and lick the ovary with their labellæ, and then climbing up the anthers, dust the soles of their feet or the whole under-surface of their bodies with pollen. So, flying away to other flowers, they accomplish cross-fertilisation (589).

*Veratrum album*, L., is proterandrous. Some plants possess, in addition to the hermaphrodite flowers, male flowers also; others



unsymmetrical curvature of the reproductive organs especially of the style.

The colour of the perianth in Liliaceæ must originally have been greenish, as it still is in Paris, while the flowers at first made themselves conspicuous to insects by the colour of the reproductive organs. By the selective agency of short-lipped insects, those flowers which had freely-visible honey, and then such as had their honey partially concealed, developed greenish-yellow colours (*Veratrum*), yellow (*Tofieldia*, *Gagea*), greenish-white and white (*Lloydia*, *Anthericum*), and their perianth-segments became devoted to purposes of display. It was only when sand-wasps, bees, long-tongued flies and Lepidoptera began to play a leading part as the fertilising agents, and led to the development of flowers that were no longer accessible to the great host of short-lipped visitors, that red, violet, and blue colours began to be developed through the higher colour-sense of these insects. In the genus *Allium*, for instance, the species with more accessible honey (*A. ursinum*, *A. victoriale*) have a white perianth; those with less accessible honey, which are visited chiefly by sand-wasps and bees, and also by Lepidoptera and long-probosced flies (e.g. *A. rotundum*), have the perianth red. In Liliaceæ, as in other cases, the flowers which are fertilised by bees have by far the greatest variety of colour, as we see by a glance at *Tulipa*, *Fritillaria*, *Scilla*, *Muscari*, *Hyacinthus*, *Asparagus*, and *Convallaria*. The colours of those which are fertilised by Lepidoptera are far less various. *Lilium bulbiferum*, which is fertilised by diurnal Lepidoptera, is clothed in fiery red; *Paradisica*, which is adapted for nocturnal species, is white; *L. Martagon*, which only became modified for Sphingidæ supplementarily, has exchanged its bright colours for dull ones since it ceased to be fertilised by diurnal Lepidoptera (609, pp. 55, 56).

#### ORD. AMARYLLIDÆ.

396. *GALANTHUS NIVALIS*, All.—Sprengel has given a full, and on the whole accurate, account of this flower; he was, however, inaccurate in regard to the structures which he supposed to shelter the honey, and his account is incomplete in regard to the circumstances which favour cross-fertilisation.

The green parts of the grooves on the inner surface of the inner petals secrete and lodge the honey, which is sufficiently sheltered from rain by the pendulous position of the flower. As

Sprengel has correctly stated, the six anthers, which lie close round the style, dehisce by apical slits, and when touched permit a little pollen to fall out; each anther sends a process outwards towards the perianth, but this is not at all a contrivance to guard the honey from rain, but a very important arrangement favouring cross-fertilisation. For when an insect tries to reach the honey, it cannot avoid touching one or more of these anther-processes, and so causes the pollen to be shaken out upon its head. The style projects beyond the anthers, and the insect therefore touches the stigma before it gets dusted with the pollen of the flower. In case of insect-visits, cross-fertilisation is thus ensured; but in absence of insects self-fertilisation is apt to take place by pollen falling on the stigma.

The hive-bee visits the flowers diligently in sunny weather, as Sprengel observed, alighting on one of the outer perianth-segments. If in search of pollen, it thrusts its head, forelegs, and midlegs into the flower, clinging by means of its hindlegs to the outer surface of an inner perianth-segment. With the tarsal brushes of its fore and mid-legs it sweeps pollen from the anthers, and places it in the baskets on its hindlegs. If it wishes to suck honey, it usually finds it more convenient to use its fore and mid-legs for clinging to the perianth. In either case the bee's head may always be found covered plentifully with pollen.

*Narcissus Tazetta*.—Delpino thinks that this species is chiefly fertilised, like many other Amaryllideæ, by nocturnal or crepuscular Lepidoptera. However, he has directly observed it to be visited by *Anthophora pilipes* (177, p. 59).

*Crinum*.—A species with white, sweet-scented flowers, about seven inches long, is believed by Delpino to be fertilised by butterflies and by honey-sucking birds in its native country, and by butterflies in Florence. He found butterflies' scales upon the stigma, and saw good seed repeatedly borne by the flowers. The essential organs are exerted, and the stigmatic surface is not exposed until the anthers have withered (177, p. 56).

*Pancreatium maritimum*.—The honey is very deeply situated, and the flower seems to be adapted for *Sphinx Convolvuli* by which it is very frequently visited (172, p. 17; 352, p. 794).

#### ORD. TACCACEÆ.

*Tacca (Ataccia) cristata*.—The flower, in Delpino's opinion, has a similar mechanism to that of *Aspidistra elatior* (178, 360).

ORD. *DIOSCOREACEÆ*.

*Dioscorca*.—The species which are cultivated in South Brazil and propagated there asexually, never, with one exception, produce flowers (359).

ORD. *PONTEDERIACEÆ*.

*Pontederia* is remarkable as a trimorphic monocotyledon. My brother Fritz Müller found only long-styled and short-styled individuals of an apparently trimorphic species of *Pontederia*, on the banks of the Itajahy-mirim in South Brazil; while another species, *P. (Eichornia) crassipes*, which has been introduced as an ornamental plant into the colony of Blumenau, exists there in long-, mid-, and short-styled individuals (556).

*Monochoria*, L., has cleistogamic flowers, according to Kuhn (399).

ORD. *COMMELINACEÆ*.

Weinmann has observed subterranean cleistogamic flowers in *Commelina bengalensis* (531).

*Tradescantia erecta* produces cleistogamic flowers in Kew (330).

ORD. *JUNCACEÆ*.

*Juncus* and *Luzula* have anemophilous flowers in which self-fertilisation is for the most part rendered impossible by proterogyny. The proterogynous flowers of *Luzula pilosa* have been figured by Hildebrand (351, fig. 4), those of *Juncus filiformis* by Axell (17, p. 38). So far as their proterogynous condition is concerned, the flowers of *Luzula campestris* agree perfectly with those of *L. pilosa*.

*Juncus bufonius*, according to Batalin (39), is exclusively self-fertilised in Russia, the flowers, which are triandrous, remaining closed. According to Ascherson (10), the same species at Halle has ordinary open, lateral, hexandrous flowers, in addition to terminal cleistogamic, triandrous ones. This statement is confirmed by Haussknecht,<sup>1</sup> who found hybrids between *J. bufonius* and *J. sphærocarpus*, whose flowers always expand fully.

*Luzula lutea* and *L. nivea* attract insects by their conspicuous

<sup>1</sup> *Botanische Zeitung*, p. 802, 1871.

colour; the former shows in other respects also remarkable approximations to the condition of an entomophilous flower. Indeed, if the pollen-grains of *L. lutea*, instead of being smooth and powdery, became adhesive, the plant might be supposed to have attained the rank of an entomophilous species (609, fig. 1).

#### ORD. PALMÆ.

*Sabal Adamsoni* has a white perianth which contains honey; it is proterogynous and is fertilised by insects (*Halictus*, *Polistes gallica*). *Chamædorea* is also entomophilous; *Cocos* and *Syagrus*, on the other hand, are anemophilous (177, p. 61).

#### ORD. AROIDEÆ.

397. *ARUM MACULATUM*, L.—The arrangement of the flowers in this species agrees so completely with Delpino's excellent account of *Arum italicum* (178, 360) that I have little new to add. The upper part of the spathe (*d*, 1, Fig. 185) serves as a wide, conspicuous entrance, guiding small Diptera (*Psychoda*) into the lower chamber (*c*) which forms a temporary prison. The insects creep down the dark-red spadix (*e*) or sometimes the sides of the spathe until they reach the upper part of the chamber (at the level of *a*, *b*, 1, Fig. 185). At this point several rows of hairs (metamorphosed stamens) radiate outwards, pointing slightly downwards, from the spadix, and form a palisade which does not prevent the small visitors from creeping down into the chamber (*c*), but afterwards prevents them from escaping when they try to fly towards the light. Even when they try to escape by crawling up the spadix, the sharp downturned points bar their way.

In the first stage of flowering the stigmas only, which are borne by the base of the spadix, are mature; a foul ammoniacal smell attracts the *Psychodæ* into the prison, where they cross-fertilise the stigmas if they have come from other plants. In the second stage the stigmatic papillæ wither, and a drop of honey appears in the middle of each stigma, to reward the little visitors for their pains. In the third stage the anthers dehisce, and the greater part of their pollen falls upon the floor of the chamber; the insects dust themselves over and over with it, and finally, when the palisade of hairs withers in the fourth period, they pass out, and enter another flower in its first stage.

Delpino has observed *Arum italicum* to be fertilised by six different flies, of the genera *Ceratopogon*, *Chironomus*, *Sciara*, *Psychoda*, *Limosina*, and *Drosophila* (178, p. 243). In *Arum maculatum* I have only found *Psychoda*, but it occurs almost constantly, and sometimes by hundreds in a single spathe. I could often see, on looking down through the grating, that many of the prisoners were trying to fly upwards to the light, and falling backwards, or trying to crawl out and being repulsed by the sharp points. Whenever I broke open a spathe in the third

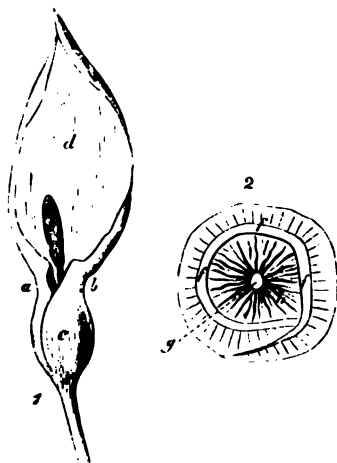


FIG. 185.—*Arum maculatum*, L.

- 1.—The whole inflorescence.  $\times \frac{1}{4}$ .
- 2.—Transverse section at the level of *ab* (1), seen from above, on a somewhat larger scale.  
*ab*, point at which the cage *c* is closed by stiff hairs, radiating from the spadix; *c*, cage inclosing the spadix with its reproductive organs; *d*, attractive portion of spathe; *e*, barren portion of spadix, serving as a guide-post; *f*, cross-section of spathe; *g*, ditto of spadix; *h*, stamens transformed into stiff filaments.

stage of flowering, I always found a multitude of inmates groping about in the thick layer of pollen on the floor of the chamber. The *Psychodæ* which I collected were so various in size and colour that I supposed I had obtained at least three species; but Herr Winnertz of Crefeld tells me that they all belong to the very variable species *Psychoda phalænoides*, L., which is probably the same species found by Delpino in *Arum italicum*, and identified by Rondani as *Psychoda nervosa*, Schr.<sup>1</sup>

<sup>1</sup> According to Schiner, *Psychoda phalænoides*, L., is identical with *P. nervosa*, Mgn., and perhaps also with *Tipula nervosa*, Schrank.

Peyritsch, from Central Africa, remain with their inflorescence, which consists of male and female flowers, and is inclosed within a spathe (like our *Arum*), beneath the ground; the tip only protrudes, and by it the fertilising agents creep into the floral chamber. A similar condition exists in *Biarum* and *Cryptocoryne* (222).

*Calla palustris*, L.—This plant exhibits a first step towards the condition of things which is perfected in *Arum maculatum*. Its disgusting smell protects it from injurious animals, and attracts carrion-loving flies. The white spathe is very conspicuous, and the proterogynous condition is very distinctly marked (590, 1.). Eug. Warming (762) attributes a share in the work of fertilisation to pond-snails.

*Symplocarpus fœtidus*.—This shows an intermediate stage between the open spathe of *Calla palustris* and the closed prison of *Arum maculatum* (728).

In *Ambrosinia Bassii* the anthers are within the spathe, the stigmas outside, at the end of the spadix. The fertilising agents (flies) creep down the spadix, and so in each plant come in contact with the stigmas before the anthers (178, p. 230).

*Anthurium Pothos* is proterogynous with short-lived stigmas, like most other Aroideæ (177, p. 62).

#### ORD. LEMNACEÆ.

*Lemna minor*, L., according to Ludwig, is adapted for fertilisation by insects which live upon the surface of the water; so also, apparently, are *L. trisulca*, *L. gibba*, and *L. polyrrhiza* (435).

#### ORD. ALISMACEÆ.

398. *ALISMA PLANTAGO*, L.—The three white or reddish petals are yellow at the base, and expand to form a disk about 10 mm. in diameter.

The chief visitors are Syrphidæ. They alight sometimes in the middle of a flower, in which case the insect's belly comes in contact with the stigmas and immediately afterwards with the anthers; or they alight on one of the petals and creep towards the pollen or honey, in which case various parts of the insect's body come in contact with the anthers, and sometimes also with the stigmas.

Although the possibility of self-fertilisation being effected by the insect-visitors is by no means excluded, cross-fertilisation is very much more probable, for when the insect alights in the middle of the flower cross-fertilisation is inevitable, and even if it alights on a petal cross-fertilisation is more likely to occur than self-fertilisation owing to the relative position of the anthers and the drops of honey.

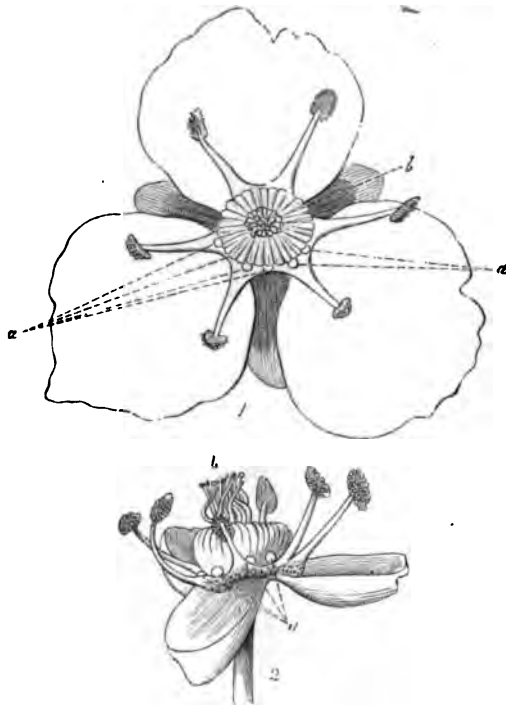


FIG. 186.—*Alisma Plantago*, L.

- 1.—Flower, seen from above.
  - 2.—Ditto, in side view, after removal of the petals.
- a, honey-drops; b, stigma.

The six anthers are directed obliquely upwards and outwards, and dehisce extrorsely. They stand at a considerable distance from the stigmas, which project in the middle of the flower and ripen simultaneously with them. Honey is secreted in twelve drops by the inner surface of a fleshy ring formed by the coherent bases of the filaments; one drop is placed opposite to each filament, and one in the interspace between each pair (a, 1, 2,

Fig. 186). A fly, starting from a petal, usually applies its tongue to the honey-drops one by one, and after each it strokes an anther with its labellæ; in so doing it may bring various parts of its body in contact with the anthers; but, as a rule, the parts which come in contact with the anthers are not those which come in contact with the stigmas in the same flower.

I have not determined whether self-fertilisation takes place in absence of insects.

Visitors : Diptera—*Syrphidæ* : (1) *Eristalis sepulcralis*, L. ; (2) *Syritta pipiens*, L., both ab. ; (3) *Ascia podagrica*, F., very freq. ; (4) *Melanostoma mellina*, L. ; (5) *Melithreptus scriptus*, L. ; all sometimes sucking, sometimes eating pollen.

*Alisma natans*, L.—In floods, the flowers remain closed below the surface of the water, and fertilise themselves (351).

#### ORD. *NAIADACEÆ*.

The plants of this order are anemophilous or hydrophilous.

The proterogynous flowers of *Triglochin palustre*, L., have been figured by Axell (17).

The species of *Potamogeton* are distinctly anemophilous. The proterogynous flowers of *P. perfoliatus*, L., have been figured by Axell (17, p. 38).

*Posidonia* is supposed by Delpino to be a grass adapted for a submerged life (178).

*Zostera* is considered by Delpino to be an Aroid modified for a submarine existence (178, II.). The mode of fertilisation of *Zostera marina*, L., is described by Clavaud (138) and Engler (223).

#### ORD. *CYPERACEÆ*.

The plants of this order are throughout anemophilous, but, like the grasses, they are by no means without occasional insect-visits. I have very often seen *Melanostoma mellina*, L., busy on the anthers of *Scirpus palustris*; my son Hermann has seen several specimens of the hive-bee collecting pollen on *Carex hirta*, L., and I have watched the same insect doing so on *Carex montana*, L.



## PART IV.

### GENERAL RETROSPECT.

IN this section I propose to review the various structural features of flowers that have already been described in detail, and to trace their general effect on the life of the plant. If we cannot discover the causes, we may determine accurately the effects, of any modification in structure of a flower.

The various characters of entomophilous flowers which affect the life of the plant may be grouped as follows :—

1. Characters which influence the visits of insects—
  - a. General attractions for anthophilous insects.
    - a. Colour or scent.
    - β. Honey, pollen, shelter, or other substantial benefit.
  - b. Increased attractions for certain insects, gained by the exclusion of others.
    - a. By colour or scent.
    - β. By concealment of the honey or pollen.
    - γ. By the time of flowering or the place of growth.
2. Characters which influence fertilisation—
  - a. Mutual adaptations of pollen and stigma.
  - b. The insuring of cross-fertilisation in case of insect-visits, and of self-fertilisation in absence of insects.

#### 1.—a. CHARACTERS INDUCING INSECTS' VISITS.

##### a. *Effect of Conspicuousness and of Odour.*

IN the third section of this book, I have discussed so many cases of closely allied flowers differing in conspicuousness, and at the same time in abundance of insect-visits and in the chances

their reach. For instance, butterflies may be seen on the honeyless flowers of *Hypericum perforatum*, applying their tongues to the base of the flower without either finding honey or piercing succulent tissue; the hive-bee tries in vain to reach the honey of *Iris Pseudacorus*, and *Rhingia* to reach the honey of *Dianthus deltoides* and *Lamium maculatum*. *Bombus terrestris* tries vainly to reach the honey of *Aquilegia vulgaris*, *Primula elatior*, *Vicia Faba*, etc., in the legitimate way, but finally bites a hole and steals the honey; various small insects (*Meligethes*, *Andrena parvula*, *Spilogaster semicincta*) visit the flowers of *Cypripedium*, but find no food and, being unable to escape, are starved to death. I think I have given enough similar instances in foregoing pages to prove beyond doubt that anthophilous insects are not guided by hereditary instinct to particular flowers.

Another class of facts shows clearly that those insects whose bodily organisation is least adapted for a floral diet, are also least ingenious and skilful in seeking and obtaining their food; so that anthophilous insects intelligence seems to advance *pari passu* with structural adaptation. This statement is fully proved by the insect lists given in the sequel. The following examples may serve to illustrate the point at present. *Coccinella septempunctata*, which is not adapted at all for a floral diet, behaves so awkwardly on flowers of *Erodium cicutarium* that it generally loses its hold and often falls to the ground; and many attempts fail to make it more skilful. *Sarcophaga carnaria* seeks honey diligently on flowers of *Polygonum Bistorta*, but it usually misses its aim in trying to insert its proboscis into the flowers; *Andrena albicans* at first is equally awkward, but gradually becomes more skilful and learns to insert its proboscis with greater accuracy. The hive-bee never fails in any case to insert its proboscis accurately.

Since we have found that structural adaptation and intelligence advance together, it is easy to understand the fact that short-lipped insects, little or not at all specialised for a floral diet, can usually only find fully exposed honey, such as *Listera*, *Parnassia*, *Cornus*, and *Umbelliferae* afford; honey still easily accessible but not directly visible to them is passed by. It is also quite intelligible that the more specialised visitors visit those flowers most diligently which supply them with most booty; for instance, bees furnished with abdominal collecting-brushes visit chiefly flowers fitted to apply pollen to their ventral surfaces; long-tongued bees visit chiefly flowers with deep honey-receptacles, whose honey is inaccessible to the great mass of insects; and hawk-moths, which

surpass all other insects in length of tongue, visit flowers whose honey is accessible to them alone.

We find that the above-mentioned insects often resort, to a certain small extent, to flowers less productive than those that they usually frequent. It is rare for a plant which produces numerous flowers and much honey or pollen to continue so abundant for the whole period that an insect is on the wing that that insect can confine its visits to it alone. In such cases it is probable that the acquired habit is transmitted instinctively from one generation to another.

The study of particular species of insects confirms the conclusion based on observation of the more conspicuous flowers, that in general anthophilous insects are not confined by hereditary instinct to certain flowers, but fly about seeking their food on whatever flowers they can find it. And hence the circumstance, already insisted on, that a flower receives the more visits the more conspicuous it is, becomes readily intelligible. It is also clear how natural selection must have seized upon and perpetuated all characters tending to greater conspicuousness. And thus we may explain all such phenomena as the development of various colours in flowers, the enlargement and increased prominence of the coloured surfaces, the association of many flowers together, the division of labour in such associations between reproductive and merely attractive members of the community, the appearance of the flowers before the leaves in *Salix*, *Cornus mascula*, etc., and many other similar phenomena.

#### *Effect of Odour.*

The effect of various perfumes in attracting insects is as manifest as the effect of conspicuousness; and observation shows that strong scent is an even more powerful lure than bright colours. The richly scented flowers of *Convolvulus arvensis* are far more abundantly visited than the larger and more conspicuous but scentless flowers of *C. sepium*; the sweet-scented Violet is much more visited than the large, brightly coloured, but scentless Pansy; the small, insignificant, but strongly perfumed flowers of *Lepidium sativum* surpass in the abundance of their visitors the other more conspicuous but scentless Crucifers.

#### *β.—The Effect of Food Supply.*

Every plant supplies in its pollen a nitrogenous food which is readily made use of by many insects, and when once found leads

to repeated visits. Hence even well-marked anemophilous flowers are often visited by insects.<sup>1</sup>

This fact is of special importance in explaining the origin of entomophilous flowers. For the fact that the lowest and most primitive Phanerogams are anemophilous forces us to suppose that all entomophilous plants have sprung originally from anemophilous; that the first adaptations to insect-visits were attained in flowers adapted for wind-fertilisation; and that wind-fertilised flowers, then as now, received visits from insects. In comparatively few entomophilous flowers is the amount of pollen required by the plant itself the sole attraction for insects. The great majority either produce a large excess of pollen or else secrete honey. The fact that many plants<sup>2</sup> secrete honey even outside their flowers, in which case it does not influence fertilisation, renders it probable that the mere excretion of honey is beneficial, and may have begun before all adaptations to insect-visits. Whether the excretion of honey began before or after the first adaptations to insect-visits, honey is now the most powerful attraction for insects. If we compare the insect-visits of *Genista* and *Lotus*, of *Helianthemum vulgare* and *Ranunculus acris*, *R. repens*, or *R. bulbosus*, of *Spiræa filipendula* or *S. Ulmaria* with *S. salicifolia*, *S. ulmifolia*, or *S. sorbifolia*, we perceive how much more abundant visits (*cæteris paribus*) a flower which contains honey receives than a similar flower which does not, and how much more various are the insect-visitors if the honey is easily accessible.

A third food material which leads insects to repeated visits is sap included within succulent tissues. Darwin's observations and my own have shown beyond the possibility of doubt that the inner membrane of the spur of our native Orchises is pierced by insect-visitors. I have shown that the same is probably true of *Cytisus Laburnum*, and *Erythræa Centaurium*. The circumstance that many flies (*Empidæ*, *Conopidæ*, *Bombylidæ*), as well as the more specialised bees and Lepidoptera, are provided with a boring apparatus at the tip of their proboscides, indicates that this boring for sap is much more usual among insects than was formerly supposed. From the comparatively few visits which our Orchises receive it would appear that sap included within a tissue is less attractive to insects than free honey.

Anthers, filaments, petals, carpels, in short all the more delicate

<sup>1</sup> See *Poterium*, p. 236; *Artemisia*, p. 333; *Cupuliferæ*, p. 523; *Cyperaceæ*, *Gramineæ*, p. 567.

Cf. *Vandinæ* and *Epidendrînæ*, p. 528.

flowers, even though they are scentless and offer no honey, or none that is accessible (*Ranunculus*, *Helianthemum*, *Papaver*, *Genista*), attract beetles in numbers. The only apparent explanation of these facts is that beetles are only or mainly attracted to flowers by bright colours. If this explanation is correct, dull-yellow must be an advantageous colour for plants with freely exposed honey, protecting them from these injurious guests. And the fact that dull-yellow colours only occur in flowers with exposed honey lends support to this view.

Delpino goes much further in regard to the exclusion of insect-visitors by colour, for he supposes that dull-yellow and purple-spotted flowers are visited only by Diptera. But my lists show that almost all the dull-yellow flowers mentioned above are visited by Hymenoptera, sometimes in great abundance and variety. I have only investigated two purple-spotted flowers, namely, *Cypripedium Calceolus*, whose staminode is speckled with purple, and *Lycopus europæus*, whose lower lip bears reddish-purple spots; but both of these are visited chiefly by insects of other orders.

Indirect limitation of insect-visitors by colour is instanced in several other cases; but such limitation is of very subsidiary importance, since it is always combined with other more powerful restrictions. Several bright and pretty flowers, *e.g.* the species of *Dianthus*, attract butterflies in great numbers; even if the honey was accessible to other insects their visits would be greatly reduced by the fact of the honey being in great part used up by the butterflies; but in these cases the honey is placed at the bottom of a tube so narrow that it is only accessible to the proboscis of a butterfly.

Many light-coloured flowers, which often grow in shady places, are inconspicuous by day but conspicuous by night (*e.g.* *Platanthera*). These are chiefly visited by crepuscular Lepidoptera, but insects are excluded not so much by the colour as by the situation of the honey at the base of long, narrow tubes.

Limitation of insect-visits by peculiar odour is probably a more common phenomenon; but our present knowledge is not sufficient to admit of perfectly definite conclusions. It is obvious that flowers with a putrid odour are mainly fitted to attract carrion-flies and meat-flies, but how far their odour repels other insects has not yet been decided by observation. None of our native flowers possess odours of this kind. In like manner it is scarcely possible to doubt that the foul ammoniacal smell of *Arum* is

entirely removed; the disadvantage is not directly visible, is in spots or lines), which point more intelligent visitors to finding deeply placed honey is convenient standing-places, of insect's head or proboscis (The grouping of many flowers in rapid passage from flower to flower). Finally, in *Scabiosæ* and *Compositæ* the exerted reproductive organs are rendered not incompatible with

In the account that I have given of flowers with more or less deeply placed honey, in the first place, the advantages were the protection of the honey from accumulating a large store; and for insects was an advantage obtained. I suggested that possibly this statement of the long proboscides of anthophilous flowers have been advanced together to must suppose that the first honey was on flat surfaces, and that flowers were only furnished with organized honey. Under these conditions the proboscis would be of no advantage, there was only freely exposed honey and increased room for accumulation to the plant even before insect

flowers, that it became possible for long-probosced varieties of entomophilous insects to vanquish their short-lipped relatives in the struggle for existence. This tendency of natural selection must have taken effect the more certainly, in each class of insects, the more the insects were dependent on a floral diet.

To give a clear view of the effect of simple concealment of the honey in flowers with exposed anthers, I have tabulated the visitors of certain groups of flowers in which the honey is fully exposed, others in which it is more deeply situated but still visible, and others again, in which it is quite concealed. The following is a summary of the result :—

(a) On the twenty-five Umbelliferæ treated in detail in Part III., whose flowers contain honey freely exposed in a smooth, adherent layer, I have observed 757 distinct insect-visits; that is to say, an average of 30 to each species.

(b) On thirty-eight species of flowers whose honey is still visible, but is placed more or less deeply at the base of a regular flower, and accumulates in somewhat greater quantity (*Cruciferae*, Nos. 27—41; *Polygonum*, Nos. 369—374; *Alsineæ*, Nos. 60—67; *Rosaceæ*, Nos. 128, 133, 135, 150—153), I have observed 582 distinct insect-visits, or on an average 15 to 16 to each species.

(c) On twenty-seven species of flowers whose honey is not directly visible but is yet accessible to the most short-lipped insects (*Geraniaceæ*, Nos. 76—83; *Malva*, Nos. 69—72; *Epilobium*, No. 166; *Campanula*, Nos. 277—282; *Jasione*, No. 283; *Ranunculus*, Nos. 6—10) I have observed 384 distinct insect-visits, or an average of 13 to 14 to each species.

If we classify these visits according to the classes to which the insects belong, and subdivide these classes, when necessary, according to the lengths of the insects' proboscides, we find the following number per thousand visits, for each of the above-mentioned group of flowers :—

- (1) *Orthoptera*, *Neuroptera*, and *Hemiptera* : (a) 12; (b) 3; (c) 3.
- (2) *Coleoptera* : (a) 84; (b) 168; (c) 76.
- (3) Long-tongued *Diptera* : (a) 84; (b) 167; (c) 78.
  - Bombylius*, *Empis*, and *Conopidæ* : (a) 15; (b) 40; (c) 26.
  - Eristalis*, *Helophilus*, and *Volucella* : (a) 69; (b) 105; (c) 36.
  - Rhingia* : (a) 0; (b) 22; (c) 16.
- (4) Short-tongued *Diptera* : (a) 289; (b) 250; (c) 180.
- (5) *Apidæ* : (a) 127; (b) 292; (c) 524.
  - Prosopis* : (a) 25; (b) 14; (c) 42.
  - Sphecodes*, *Andrena*, and *Halictus* : (a) 86; (b) 175; (c) 250.
  - Other bees with moderately long tongues : (a) 15; (b) 70; (c) 180.
  - Bombus* and *Anthophora* : (a) 1; (b) 33; (c) 52.
- (6) Other *Hymenoptera* : (a) 332; (b) 69; (c) 91.
- (7) *Lepidoptera* : (a) 8; (b) 41; (c) 44.
- (8) *Thrips* : (a) 0; (b) 10; (c) 5.

However imperfect my lists may be, and however small the value that we can give to particular numbers, this table shows clearly that with increased

concealment of the honey the number of short-lipped visitors diminishes and the number of long-tongued visitors increases; and that, in the end, bees far outnumber beetles, wasps, and short-lipped flies.

The tubes in which various flowers conceal their honey vary in length between very wide limits—from scarcely 1 mm. to about 30 mm. in our native flowers. In the shortest forms, *e.g.* species of *Veronica*, the tube with its interior circle of hairs acts just like the structures which shelter the honey in *Malva* and *Geranium*. The further increase of length in such tubes depends entirely upon the advantage to the flower of excluding certain groups of insects in order to induce more diligent visits on the part of others.

If increase in length of the proboscis proceeded *pari passu* with increased need of food and increased diligence, and therefore also with increased usefulness in the work of fertilisation, the various adaptations connected with it would be comparatively easy to understand. But this is by no means the case. The entomophilous insects which require most food and are most diligent, and therefore the most efficient fertilisers, are unquestionably the Bees, since they feed not only themselves but their young solely on substances derived from flowers; but the circumstance that they have to use their mouth-parts to build the cells for their young has set definite limits to the adaptation of these parts for obtaining deeply placed honey, while such limits do not exist for *Lepidoptera*. Accordingly, though bees have far surpassed flies in the length of their tongue (our longest-tongued *Diptera*, *Bombylius* and *Rhingia*, have proboscides 10 to 12 mm. long, while *Anthophora pilipes* and *Bombus hortorum* have proboscides over 20 mm. long), they are far outstripped by many *Lepidoptera* (*Sphinx ligustri*, 37 to 42 mm., *S. Convolvuli*, 65 to 80 mm.).

Though, owing to the special diligence of bees, most tubular flowers have elongated their tubes so as to exclude the more short-lipped insects and to admit a wider or narrower circle of the more specialised bees, and though many of these flowers are shown by other structural adaptations to be specially fitted for bees, yet butterflies have access to the honey of all these flowers, and sometimes act as subsidiary fertilising agents though often they are quite useless to the plant.

Most of our native flowers with hidden honey have at the same time their pollen more or less deeply situated, or else differ in other important relations, and are therefore not fitted to show clearly the effect of increased concealment

of the honey. The *Compositæ*, however, furnish several series of forms well fitted to demonstrate this point. Omitting some aberrant forms, the honey is on the whole least deeply situated in the *Senecionidæ*, more deeply placed in the *Cichoriaceæ*, and most deeply in the *Cynareæ*. On (a) ten *Senecionidæ* (Nos. 216, 222, 224, 226, 227, 228, 232, 233, 236, 237), I have observed 335 different insect-visits, or an average of 33·5 to each species; on (b) fifteen *Cichoriaceæ* (Nos. 259, 261—273, 275), 356 distinct visits, or an average of 23 to 24; and on (c) ten *Cynareæ* (Nos. 240, 241, 244, 245, 249, 252, 254, 256, 257, 258), 189, or an average of 18 to 19. The following table is similar to the preceding one, and shows the proportionate number of visits paid by each group of insects, reckoning the total number of visits observed at 1,000.

- (1) Specially long-tongued bees, *Bombus* and *Anthophora* : (a) 15 ; (b) 48 ; (c) 211.
- (2) Bees with abdominal collecting-brushes (and long proboscides) : (a) 27 ; (b) 48 ; (c) 131.
- (3) Other bees with long or moderately long proboscides : (a) 42 ; (b) 126 ; (c) 85.
- (4) *Sphecodes*, *Andrena*, and *Halictus* (proboscides moderately long) : (a) 167 ; (b) 399 ; (c) 196.
- (5) *Prosopis* and *Colletes* (short-tongued) : (a) 30 ; (b) 8 ; (c) 5.
- (6) Other *Hymenoptera* (mostly short-lipped) : (a) 137 ; (b) 17 ; (c) 35.
- (7) Long-tongued, purely suctorial *Diptera* (*Bombylius*, *Evipis*, *Conopidæ*) : (a) 42 ; (b) 42 ; (c) 35.
- (8) *Rhingia* : (a) 3 ; (b) 3 ; (c) 10.
- (9) *Syrphidæ* with shorter tongues than *Rhingia* (*Eristalis*, *Helophilus*, *Volucella*) : (a) 92 ; (b) 84 ; (c) 55.
- (10) Short-tongued *Diptera* : (a) 242 ; (b) 121 ; (c) 10.
- (11) *Lepidoptera* : (a) 80 ; (b) 67 ; (c) 171.
- (12) *Coleoptera* : (a) 116 ; (b) 34 ; (c) 45.
- (13) *Hemiptera* and *Panorpa* : (a) 9 ; (b) 3 ; 10.

This table proves clearly that in *Compositæ* as the honey becomes more deeply placed the visits of the more highly specialised bees increase, while, in spite of the exposed situation of the pollen, the visits of flies fall off. This is true of the number of species of visitors; but if it were possible to record the number of visits paid by each species, the preponderating influence of bees would be still more apparent. From these first stages in elongation of the corolla-tube and increase of bees' visits by exclusion of short-lipped insects, we pass by the most gradual steps to the exceedingly long tubes whose honey is monopolised by a smaller and smaller number of bees. At the top of the series stand flowers whose tubes are 16 to 20 mm. long, and whose honey is only accessible to a few species of *Bombus* and *Anthophora* (*Aquilegia*, *Delphinium*, *Pedicularis*, *Lamium maculatum*, etc.).

It would not be possible without many more observations to classify our flowers in a long series of groups, each one restricted to a smaller circle of bees. The length of the tube is not of itself a measure of the proboscis necessary to reach the honey; for often the mouth of the flower is widened to admit the insect's head or even part of its body, and further the honey often accumulates to a considerable depth in the tube. Such conditions are illustrated in many *Sileneæ*, *Boragineæ*, *Scrophulariaceæ*, *Ericaceæ*, etc.

rather more numerous bees can do so. The pollen is most completely protected in those flowers whose stamens are completely shut up within the corolla (*Fumariaceæ*, *Papilionaceæ*, *Rhinanthus*, *Melampyrum*, *Pedicularis*, *Salvia*), or whose pollen is united in masses and enclosed in pouches (*Asclepiadeæ*, *Orchideæ*). These plants are no longer able to have their pollen transported by miscellaneous insects, but they have developed adaptations of the most perfect kind for cross-fertilisation by certain special insects.

The mechanism is so perfect and so effectual in these flowers that cross-fertilisation is thoroughly insured, though some of them offer only pollen to their visitors (*Genista*, *Sarothamnus*), others pollen and sap (*Cytisus*), others sap only (*Orchis*).

The contrivances that we have just reviewed give to two divisions of anthophilous insects exclusive or almost exclusive access to the food materials contained in certain flowers; namely, in most cases to bees, which, however, must usually share their honey with the Lepidoptera; and in relatively few cases to Lepidoptera, when, if the pollen lies exposed, flies may devour it and bees collect it, playing a subsidiary part in the work of fertilisation. But certain small Diptera which resort to small dark cavities have a much more complete monopoly of those flowers which furnish them with such temporary abodes, and which have become adapted for cross-fertilisation by them (*Aristolochia Clematitis*, *Arum maculatum*); for the narrow entrance usually excludes all other insects.

*Limitation of Insect-visits by Time of Flowering and by Place of Growth.*

It is obvious that every species of flower can only be visited and fertilised by those insects which occur at the time when the plant is in flower, and in the stations where it grows. The insect-visitors of a plant are therefore limited by the season and by the time of day when it flowers, by its geographical distribution, and by the nature of its habitat.

We may assume, furthermore, with Delpino (175 A), that the geographical range of many flowers finds its limit where insects suitable for their fertilisation begin to fail. But the particular cases which Delpino adduces to support this view are, in part, based on insufficient observations.<sup>1</sup> Our stock of observations is

<sup>1</sup> Thus Delpino supposes that the geographical range of Roses is determined by the occurrence of *Cetonia* and *Glaphyridæ* (175 A, p. 18), and that *Epilobium* and *Myosotis* are exclusively fertilised by bees (p. 19). My lists contradict both of these assumptions.

of visitors, expose their pollen (but in that case their stigmas also) to short-lipped insects, which then act as subsidiary fertilising agents (cf. *Compositæ*, *Sileneæ*, *Æsculus*, *Echium*, *Enothera*, *Lonicera*, etc.). And all flowers with hidden anthers have only been able to shelter their pollen from rain in so far as they have developed other adaptations for particular visitors, which compensate for the less general access of pollen-carrying insects. For this reason, flowers with hidden pollen afford us the most conspicuous examples of adaptation in form and in dimensions to a more or less narrow circle of visitors (cf. *Orchideæ*, *Iris*, *Papilionaceæ*, some *Boraginæ*, *Labiataæ*, *Scrophulariaceæ*, *Apocynæ*, *Ericaceæ*, etc.). These adaptations are always directly concerned in insuring self-fertilisation, and therefore fall to be considered in a future section. But the more perfectly flowers are adapted for cross-fertilisation by particular insects, the more unlikely does it become that other insects visiting the flowers will effect cross-fertilisation, and the more will such visits of other insects be useless or injurious to the plant. So concealment of the pollen is useful (to a subsidiary degree) in limiting insect-visits, and this effect has now to be considered.

Concealment of the pollen in a cone of apposed anthers (*Viola*, *Borago*, *Symphytum*) hinders it from being devoured by flies and beetles, and renders it more difficult for bees to collect it; while honey-seeking bees cannot reach the honey without causing the cone to open and shed its pollen on them.

Concealment of the anthers within open tubes (*Myosotis*, *Vincu*, *Syringa*, etc.) renders it more difficult for beetles to devour the pollen, and for bees to collect it; but if the tube is wide enough (*Syringa*), the more highly developed proboscides of certain *Syrphidæ* can enter and obtain the pollen, while narrower tubes (*Myosotis*, *Vinca*) prevent all Diptera from feeding on the pollen, and only permit their visitors to obtain honey. When the tube containing the stamens is closed (*Anchusa*, *Linaria*, *Antirrhinum*), all insects except bees, Lepidoptera, and some very minute intruders are shut out both from the honey and from the pollen. Pendulous flowers with included stamens and not too wide tubes protect their honey from removal by flies (*Asparagus*, *Convallaria*) or by other insects also (*Erica*, *Vaccinium*); such flowers are therefore visited mainly or exclusively by honey-seeking insects. A vaulted structure sheltering the anthers from rain (*Iris*, most Labiates), does not prevent, but to a great extent restricts, the theft of pollen by insects; beetles are quite unable to obtain pollen so concealed, only a few of the more intelligent flies, especially *Rhingia*, and

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insufficient to show us how the circle of visitors to a particular plant is determined by the time of flowering, the nature of the locality, the competition of other flowers, and the peculiarities of structure in the flower itself.

It is obvious that flowers which only expand at night are thereby protected from the visits of all merely diurnal insects, but among our native flowers we have scarcely a distinct example of this condition. Of the flowers mentioned above as adapted for hawk-moths and nocturnal Lepidoptera, *Lychnis vespertina* expands in the evening, without, however, being completely closed by day; while the others exclude diurnal insects from their honey only by their long, narrow tubes, and specially attract hawk-moths and night-flying Lepidoptera by their colour, and by exhaling their odour most powerfully at night.

## 2. STRUCTURAL CHARACTERS WHICH AID IN FERTILISATION.

### *Adaptive Modifications of the Pollen and Stigma.*

All the characters of flowers so far discussed can only be of advantage to the plant in so much as they contribute indirectly to the conveyance of pollen by insect-visitors to the stigmas of other flowers. But this result is only possible if the pollen is of such a nature as to adhere to the insect, and if the stigma is fitted to remove it from the insect in turn.

While in anemophilous plants the pollen consists very generally of loose, smooth, and easily scattered grains, in entomophilous flowers it presents a great variety of characters, all such as to enable it to adhere to the bodies of insect-visitors; and in all cases the nature of the stigma stands in the closest relation to the nature of the pollen, and the stigma is always fitted for attaching the pollen to itself by a viscid surface or by projecting papillæ. In flowers furnished with a contrivance for scattering their pollen (several *Scrophulariaceæ*, *Ericaceæ*, etc.) the pollen is usually smooth and loose as in anemophilous plants; but it is inclosed in receptacles from which it is dislodged by a touch of the insect, and it is often directed in its fall by special hairs. In *Syringa* and *Symphoricarpos* the insect's head or proboscis is first moistened with honey, to which the pollen then adheres; in *Vinca* and *Polygala* viscid matter is secreted by the stigma, and in *Bryonia*, *Marrubium*, *Sideritis*, etc., by spherical cells of the anther which fulfils the same function. In the great majority of cases, a

the stigma is sticky enough which come in contact with insect moves away the elastic *Asclepias* all the pollen-grains a flattened mass, which becomes to an insect's claw, and is the stigmatic chamber of an left there.

The size of the pollen-gr length of the style which the in the varying size of pollen-anthers in dimorphic and trim

*Characters which insure Cross-  
and Self-Fertilisation*

If the adaptations of flower the cross-fertilisation induced render cross-fertilisation inevitable which render self-fertilisation in tag to the plant ; but only so abundance to insure cross-fertilisation regularly fulfilled, it is obvious to have the power of reproduction while leaving only a possibility insect-visits than to be cross-fertilisation insect-visits occur, but to be insects. This is the simple explanation, that " When closely-allied in structure, differ in the abundance

those which are least visited are those in which self-fertilisation is best insured.<sup>1</sup>

The comparative merits of cross-fertilisation and self-fertilisation can only be rightly considered when the actual insect-visits that the plant receives are taken into account; and only the utter neglect of this precaution can explain how Hildebrand and Axell came to directly opposite estimates of the value of the two modes of fertilisation. For Hildebrand in his *Geschlechtervertheilung* arranges the mechanisms of flowers according as they hinder self-fertilisation, and seems to consider those the most perfect in which self-fertilisation is least possible; while Axell tries to show that the highest and most perfect Phanerogams are those which regularly fertilise themselves.<sup>2</sup>

Both views are only partially correct; the truth lies between them. The law, proved by general considerations in the Introduction and by many detailed facts in the third section of this book, that cross-fertilisation is better for a plant than self-fertilisation, but that self-fertilisation is infinitely better than no fertilisation at all and consequent sterility, must modify essentially Hildebrand's conception of a law of the avoidance of self-fertilisation. And it is evident at once that Axell's idea of a single path towards perfection in the evolution of Phanerogamic flowers is altogether untenable when we review the insurance of cross- and self-fertilisation in connection with the insurance of insect-visits.

The oldest Phanerogamic flowers which adapted themselves for the transport of their pollen by insect-agency certainly possessed those characters by which insects are mainly attracted—namely, conspicuousness, perfume, and honey—to so small an extent that as a rule their insect-visitors were not numerous enough to insure cross-fertilisation. Under these conditions it must have been advantageous for the organs of both sexes to be united within one flower so as to admit the possibility of self-fertilisation. In accordance with this is the fact that while the Gymnosperms have diclinic anemophilous flowers, the great majority of entomophilous Phanerogams are monoclinic.

But as soon as in any entomophilous plant increased conspicuousness, or perfume, or food-supply had so far multiplied insect-visits that cross-fertilisation took place regularly and the possibility of self-fertilisation became quite useless, then the possibility of

<sup>1</sup> Compare *Rhinanthus*, *Lysimachia*, *Euphrasia officinalis*, *Rosa*, *Rubus*, *Epilobium*, *Geranium*, *Malva*, *Polygonum*, *Stellaria*, *Cerastium*, *Veronica*, *Hieracium*, *Senecio*, etc.

<sup>2</sup> Cf. "Historical Introduction," pp. 12, 20.

self-fertilisation could be dispensed with, and has actually in very many cases been lost. Such a result has taken place in the most diverse ways, sometimes by dichogamy, sometimes by the position of the parts in the flower, sometimes by reversion to the diclinic condition. *Asparagus officinalis*, *Ribes alpinum*, *Rhus Cotinus*, *Lychnis vespertina*, &c., are undoubted instances of plants which have reverted or are reverting from the hermaphrodite to the diclinic condition.

So when insect-visits were comparatively few it was a step towards perfection for entomophilous diclinic plants to become monoclinic; but when cross-fertilisation was insured by sufficient insect-visits the reverse transition was advantageous. So is it with all other characters which insure cross-fertilisation or self-fertilisation. Dichogamy is so general a feature throughout whole genera and orders, that it is scarcely possible to doubt that it has been inherited as an advantageous character from the common ancestors of these genera or orders; but the least conspicuous and least visited species in these groups have reverted to self-fertilisation, and in their case this reversed progress has been a step towards perfection (cf. *Senecio vulgaris*, *Malva rotundifolia*, the smaller species of *Geranium*, *Stellaria media*, etc.). In *Rhinanthus crista-galli* cross-fertilisation in the event of sufficient insect-visits is insured by the distance of the stigma and anthers from one another, and the style is elongated so that its stigma must be touched by insect-visitors; but in the less conspicuous variety the tip of the style curves backwards so far that self-fertilisation ensues without fail. It is needless to cite more of the instances already discussed, in which little-visited varieties, species, or genera fertilise themselves regularly, while closely-allied forms, more abundantly visited, have been able to dispense with the possibility of spontaneous self-fertilisation.

In my opinion, if we must describe in general terms the grades of perfection in floral mechanisms, we can only call those specially perfect which fulfil their purpose in the life of the plant specially well; that is to say, which under existing conditions insure the sexual reproduction of the species with particular success. We cannot admit that either the insurance of cross-fertilisation in case of insect-visits, or the unfailing occurrence of self-pollination, is in itself a measure of perfection in the mechanism of a flower; for both among plants which regularly pollinate themselves and among those in which spontaneous self-pollination is impossible we find numerous species which prove by their great abundance

how perfect is their structure. *Senecio vulgaris*, *Veronica hederæfolia*, *Stellaria media*, *Lamium purpureum* are examples of the one condition, and *Pedicularis silvatica*, *Malva silvestris*, and *Echium vulgare* of the other. It must by no means be supposed that all floral mechanisms are equal; in many flowers distinct imperfections have already been pointed out (*Posoqueria fragrans*, *Faramaea*, *Malva silvestris*, *Euphrasia Odontites*, *Geum rivale*, etc.). There are also species which, after abandoning the power of self-fertilisation, have suffered so from the competition of other flowers that they obtain very few insect-visits (e.g., *Ophrys muscifera*). Such instances prove still more forcibly that the uniform perfection which Axell supposes to exist in Nature has no real existence.

It may be urged that Axell proceeds from a totally different conception of perfection; for he looks upon every economy of space, time, and material as a step towards perfection; and he must therefore look upon the reversion of monoclinal flowers to dicliny, or the passage of homogamic flowers to dichogamy, as retrograde even when those changes are of distinct advantage for the sexual propagation of the plant. But such a definition of perfection is unnatural.

But even apart from any definition of perfection in a floral mechanism, nothing can be more unnatural than to assert that there is only one course of evolution or only one path towards perfection in the structure of flowers.

As in regard to conspicuousness, odour, or production and concealment of food material, so also in favouring or insuring cross-fertilisation, there is an infinite variety of means to the end. In flowers which receive abundant insect-visits cross-fertilisation has been insured sometimes by reversion to dicliny, sometimes by dichogamy, sometimes by distant separation of the stigma and pollen in the flower, sometimes by a special mechanism causing the pollen to adhere to the insect and afterwards to the stigma of the next flower. Dichogamy, though usually proterandrous, is proterogynous even in many entomophilous flowers (*Aristolochia*, *Euonymus*, many *Rosaceæ*), in spite of Axell's statement to the contrary. The separation in space of the essential organs be of the same kind in all the flowers of a species, or the relation of the parts may be different in different flowers; but in all the relative positions of the parts are closely connected with insects' visits. In the former case, when all the flowers cross-fertilisation is insured either if the same p

visitor always comes in contact first with the stigma and afterwards with the anthers (*Anthericum*, *Convallaria majalis*, *Lonicera Caprifolium*, many Labiatae, etc.), or if in each flower any part of the proboscis, body, or head of the insect touches the stigma while at the same time the opposite side touches the anthers (*Myosotis*, *Omphalodes*, *Ribes nigrum*, *Berberis*, *Cruciferae*, etc.). When the flowers are not all alike, that is to say in dimorphic (*Primula*, *Hottonia*, *Pulmonaria*, *Polygonum fagopyrum*) or trimorphic (*Lythrum*) plants, cross-fertilisation is insured if the insects touch the anthers and stigma with different parts of their bodies, but touch the stigma with that part which touched the anthers in a previous flower.

The mechanisms for applying pollen to a particular part of the insect are astonishingly various; from the nature of the case they can be the more easily attained the more the circle of visitors is restricted to a few definite forms by concealment of the honey. As examples of these multitudinous arrangements we may recall the flowers of Ericaceae, Scrophulariaceae, Boragineae, and *Galanthus*, in which pollen is sifted on to the insect; the infinite number of devices in Orchideae; and the somewhat similar mechanism of Asclepiadaceae; the flowers of Papilionaceae, Fumariaceae, and of *Lopezia*, in all of which the insect involuntarily opens the pollen-receptacle and dusts itself ventrally with pollen; *Salvia*, in which the mechanism is reversed and the insect's back receives the pollen; lastly, the simple device of the flexible stamens in *Veronica Chamædryas* and *Circæa*.

The mechanisms which have been discussed in this book are only an infinitesimal fraction of the vast variety that exists. They arose quite independently and at various times in the various divisions of those Phanerogams which had become entomophilous and monoclinic.<sup>1</sup> They have in general become developed only where increasing conspicuousness and a large supply of food material attracted so many insects that the capability for self-fertilisation became unnecessary; on the other hand, where insect-visits remained few, the power of self-fertilisation (which began with the appearance of hermaphroditism) was retained. Where cross-fertilisation that

<sup>1</sup> The mechanisms for insuring cross-fertilisation in Umbelliferae and in Compositae have been inherited from the ancestors of the order; those in the various species of *Aquilegia*, *Delphinium*, *Linaria*, and *Pedicularis*, from the ancestor of the genus; those in *Polygonum fagopyrum*, *P. Bistorta*, and *Lonicera Caprifolium*, from the ancestor of the species; while the different forms of flowers in *Rhinanthus cristagalli*, *Veronica spicata*, *Odontites scrotina*, *Euphrasia officinalis*, and *Lysimachia vulgaris*, give us examples of various floral characters being evolved within the bounds of one and the same species.

had once been insured becomes uncertain owing to the competition of other flowers (e.g. *Malva rotundifolia*, species of *Geranium*), or owing to the unfavourable locality (cf. *Lysimachia nemorum*) or unfavourable weather (cf. *Veronica Beccabunga*), the mechanisms of the flowers have in many cases undergone a change such as to render self-fertilisation again possible; in a few cases reversion to anemophily has taken place (Artemisiaceæ, *Thalictrum*). As examples of the countless ways in which plants revert to self-fertilisation in default of sufficient insect-visits, I may mention the following:—In some dichogamic flowers the stigmas curl back upon the anthers or other parts which still retain some pollen (*Stellaria graminea*, *Malva rotundifolia*, species of *Geranium*, Compositæ); the stigmas sometimes curl back till they come in the line of fall of the pollen (*Melampyrum pratense*) or even place themselves between the anthers (*Rhinanthus minor*); anthers which stand in a ring round the stigma may, in default of sufficient insect-visits, converge above the stigma, applying their pollen to it (*Myosotis*, *Lithospermum*, Cruciferae); even mechanisms which effect cross-fertilisation with astonishing precision in case of insect-visits are not unfrequently transformed so as to render self-fertilisation inevitable when insect-visits are few (certain Orchideæ, Fumariaceæ, *Salvia*); or the production of cleistogamic, self-fertilised flowers may compensate for the loss of the power of self-fertilisation in the ordinary flowers (*Viola*).

Unlike Axell, who brings his book to a conclusion by saying "We see thus that the development of mechanisms for fertilisation in Phanerogams has gone on and still goes on in the same direction,"<sup>1</sup> I should say: The dependence of entomophilous flowers on guests so infinitely various in habits, tastes, and numbers, in their food and in the means of obtaining it, must have rendered possible not one but countless paths towards perfection, paths leading not always forwards but sometimes backwards; and only in such a way could the infinite variety of existing flowers have come into existence.

My brother Fritz Müller has sent me the following instances of the general principle that whenever in a variable species selection occurs in a definite way, then that selection, apart from other relations, will lead to a continued increase of the variation in the same direction from generation to generation:—

<sup>1</sup> "Vi ansa saledes, att utvecklingen i anordningarna för könens förenig hos de fanerogama växterna fortgått och fortgår i nämnda riktning."—No. 17, p. 95.

"(1) In maize cultivated at Itajahy, the grains stand for the most part in twelve or fourteen rows, not unfrequently in ten, rarely in eight or sixteen, and very rarely in eighteen rows. In more than 100 ears which I bought for sowing in 1867 I found only one of eighteen rows. This ear produced next year 205 ears, among which were twenty-two with eighteen rows, besides one which had eighteen rows in the upper part and twenty in the lower, and one which had eighteen at the top, twenty in the middle, and twenty-two at the bottom. Next year, 1868-69, I had 460 ears obtained from seeds out of ears with eighteen rows; and of these 460, 18·2 per cent. bore eighteen rows, 4·4 per cent. bore twenty, and ·2 per cent. bore twenty-two. In the following year, among ears obtained from seed out of ears bearing twenty-two rows, one ear occurred which bore twenty-six rows.

"(2) In an Abutilon from Capivary the normal number of styles is ten. A seedling obtained from a flower with nine styles had, among 100 flowers, two with seven styles, and twenty-seven with eight; while in 100 flowers upon the mother-plant there were only three with eight, and none with seven styles.

"(3) In Abutilon there occur sometimes, but very rarely in most species, flowers with six petals.

"From seed obtained from an hexamerous flower of the hybrid *EF*,<sup>1</sup> fertilised with pollen from a pentamerous flower of the variety *F*, a plant was reared (*EF.F*) which I watched for three weeks (August 17 to September 6, 1869) counting the petals upon all the flowers that appeared on it. It bore in the three weeks:—

Flowers with 5 petals	.	.	.	.	145
Ditto " 6 "	.	.	.	.	103
Ditto " 7 "	.	.	.	.	13

"At the same time I watched another plant descended from *pentamerous* parents of the same varieties as those of the former (but obtained by pollen of the hybrid *EF* applied to the stigma of the pure species *F*). It bore in the three weeks:—

Flowers with 5 petals	.	.	.	.	454
Ditto " 6 "	.	.	.	.	6
Ditto " 7 "	.	.	.	.	0

"The simplest explanation of these facts seems to be, that each species has the property of varying within a certain amount: crossing of different individuals so long as no selection is made in a definite direction, suffices to keep the middle point fairly constant, about which the variations oscillate; and so the extremes also remain constant. But if the tendency to vary in either direction is aided by natural or artificial selection, then our middle point is as it were shifted to that side and the extremes of oscillation are also shifted towards the same side."

Since the first appearance of this work (1873) I have discussed in a series of essays the question of the Origin of Flowers and the

<sup>1</sup> *E* indicates the Abutilon called *Embira branca* by the Brazilians; *F*, an Abutilon from Pocinho (see No. 557); *EF* implies the hybrid produced by pollen of *F* applied to the stigma of *E*.

gradual attainment of their special characters. I may now close this book with a summary of my chief conclusions. The good effect of cross-fertilisation may be recognised not only in the structure of insect-fertilised flowers, but also in the water-fertilised and wind-fertilised plants which preceded them. Even in the lowest algæ we find cross-fertilisation, to effect which two individuals move towards each other in the water by means of a cilium. In a higher grade we find the two individuals differentiated, one losing its motility, and increasing in size to form an *ovum*, while the other (sperm-cell or *antherozoid*) retaining its primitive motile form swims about in quest of the ovum. This mode of cross-fertilisation is retained not only by all cellular cryptogams (except the *Floridææ* or red seaweeds, whose tailless antherozoids are moved passively in the current) but also by all vascular cryptogams. With the change to dry localities, where even occasional moisture sufficient for the migration of the antherozoids is not attainable, the vascular cryptogams seem to have developed wind-fertilised unisexual flowers; thus, first the Gymnosperms, and from these afterwards the Angiosperms have arisen.

Finally from the wind-fertilised Angiosperms, entomophilous flowers arose, as insects came first accidentally and afterwards regularly to seek their food on flowers, and as natural selection fostered and perfected every change which favoured insect-visits and thereby aided cross-fertilisation. With the transition to insect-fertilisation came, on the one hand, great economy of pollen, but, on the other hand, the uncertainty of insect-visits made it as a rule necessary that self-fertilisation should remain possible. Thus, though descended from unisexual (anemophilous) ancestors, entomophilous flowers are usually hermaphrodite, and are capable to a great extent of fertilising themselves when insect-visits fail. But in the course of further development, many of them have so increased their means of attracting insects (by colour, perfume, honey, etc.), that the power of spontaneous self-fertilisation has become superfluous and finally has been lost.

Insects in cross-fertilising flowers endow them with offspring which in the struggle for existence vanquish those individuals of the same species which are the offspring of self-fertilisation. The insects must therefore operate by selection in the same way as do unscientific cultivators among men, who preserve the most pleasing or most useful specimens, and reject or neglect the others. In both cases, selection in course of time brings those variations to perfection which correspond to the taste or to the needs of the

selective agent. Different groups of insects, according to their sense of taste or colour, the length of their tongues, their way of movement and their dexterity, have produced various odours, colours, and forms of flowers; and insects and flowers have progressed together towards perfection.

The transition from wind-fertilisation to insect-fertilisation and the first traces of adaptation to insects, could only be due to the influence of quite short-lipped insects with feebly developed colour-sense. The most primitive flowers are therefore for the most part (except, for instance, *Salix*) simple, widely open, regular, devoid of honey or with their honey unconcealed and easily accessible, and white or yellow in colour (e.g. most *Umbelliferae* and *Alsineae*, many *Ranunculaceae* and *Rosaceae*).

The carrion-loving Flies were from the first marked out by their peculiar tastes to produce certain peculiar flowers. Preferring those colours and odours which guided them to their primitive food, they produced, wherever they got special influence, dull, yellowish, or dark-purple colours, often accompanied with a putrid smell. The stupidity of flies also favoured the production of certain contrivances to insure crossing, e.g. the prison-flowers of *Arum* and *Aristolochia*, the traps of *Pinguicula alpina*, *Cynanchum*, and *Stapelia*, or the deceptions of *Paris*, *Ophrys*, and *Parnassia*.

Gradually, from the miscellaneous lot of flower-visiting insects, all much alike in their tastes, there arose others more skilful and intelligent, with longer tongues and acuter colour-sense; and they gradually caused the production of flowers with more varied colours, honey invisible to or beyond the reach of the less intelligent short-tongued guests, and various contrivances for lodging, protecting, and pointing out the honey.

Lepidoptera, by the thinness, sometimes (*Sphingidae*) by the length of their tongues, were able to produce special modifications. Through their agency were developed flowers with long and narrow tubes, whose colours and time of opening were in relation to the tastes and habits of their visitors. We may thus distinguish flowers adapted for butterflies (*Dianthus deltoides* and many *Sileneae*), or for moths (*Platanthera*); for diurnal hawk-moths (*Gentiana bavarica*, *G. verna*), for nocturnal hawk-moths (*Lonicera Caprifolium*); and intermediate stages (e.g., *Crocus vernus*). The acute sense of smell in Lepidoptera reveals itself in the aromatic scent of Pinks, *Nigritella*, *Daphne striata*, etc., and the colour-sense of butterflies is shown in the flowers, usually red and prettily marked, which are due to them.

The *Ichneumonidæ* at first surpassed all other visitors in observation and discernment, and they were thus able to produce inconspicuous flowers which escaped the notice of other visitors. On the appearance of sand-wasps and bees these inconspicuous flowers were banished by competition to the less frequented localities (*e.g.*, *Listera* to shady woods).

The Sand-wasps (*Sphegidæ*) apparently took the place to a great extent of the Ichneumons, and produced flowers where organs had to be thrust apart (Papilionaceæ), or where a narrow cavity had to be entered (Labiata), or where some other action similar to the act of digging had to be performed. Subsequently bees seem to have entered on joint possession of most of these flowers, and to have added special adaptations of their own.

The true Wasps (*Vespidæ*) could establish themselves by the fear of their sting (and of their jaws) in sole possession of certain flowers with wide open mouths and abundant honey. These they developed farther in relation to their wants (*Scrophularia*, *Symphoricarpos*, *Epipactis latifolia*, *Lonicera alpigena*); but where wasps are scarce the flowers are utilised by other insects.

Bees (*Apidæ*), as the most skilful and diligent visitors, have played the chief part in the evolution of flowers; we owe to them the most numerous, most varied, and most specialised forms. Flowers adapted for bees probably surpass all others together in variety of colour. The most specialised, and especially the gregarious bees, have produced great differentiations in colour, which enable them, on their journeys, to keep to a single species of flower. While those flowers which are fitted for a miscellaneous lot of short-lipped insects usually exhibit similar colours (especially white or yellow) over a range of several allied species, the most closely allied species growing in the same locality, when adapted for bees, are usually of different colours and can thereby be recognised at a glance (*e.g.*, *Trifolium*, *Lamium*, *Teucrium*, *Pedicularis*).

Some Drone-flies (*Syrphidæ*) also, which admire bright colours and are themselves brightly adorned (*Ascia*, *Melanostoma*, *Sphegina*, etc.), have produced special flowers suited to their tastes, which they mainly fertilise (*Saxifraga rotundifolia*, *S. umbrosa*, etc.); sometimes we even find a special and simple mechanism adapted for them (*Veronica Chamædrys*).

The power to distinguish red, violet, and blue colours must have been acquired to a certain degree by flesh-flies and carrion-flies in seeking their natural food; but in other flower-loving

insects this power seems only to have arisen with the habit of visiting flowers, and to have increased *pari passu* with the taste for flowers and with the length of the proboscis. On the whole we find red, violet, and blue colours appearing for the first time in flowers whose honey is quite concealed and which are visited by more or less long-tongued insects (bees, long-tongued flies, Lepidoptera), or else in flowers visited for the sake of their pollen chiefly by bees and drone-flies (*Hepatica triloba*, *Verbascum phoeniceum*).

The forms, colours, and odours of the flowers in a particular region must depend in the closest manner upon the insect fauna of the region, and especially upon the relative abundance in it of the various classes of insects. This conclusion is in complete accordance with the following comparison of my observations on the Alps and in North Germany. On the Alps, Hymenoptera and especially bees are relatively much less numerous and Lepidoptera much more numerous than in Low Germany.

I have observed upon flowers:—

	1. IN LOW GERMANY.		2. ON THE ALPS GENERALLY.		3. ABOVE THE LIMIT OF TREES.	
	a. Species of Insects.	b. Visits observed.	a. Species of Insects.	b. Visits observed.	a. Species of Insects.	b. Visits observed.
Coleoptera ... ..	129	469	83	337	33	134
Diptera ... ..	253	1,598	348	1,856	210	930
Hymenoptera ...	368	2,750	183	1,382	88	519
(Apidæ) ... ..	(205)	(2,191)	(120)	(1,141)	(49)	(402)
Lepidoptera ...	79	365	220	2,122	148	1,190
Other Insects ...	14	49	7	15	3	6
TOTAL ...	843	5,231	841	5,712	482	2,779

Of each 1,000 different visits observed (differing either in the species of flower visited or the species of insect visiting it) there are therefore :—<sup>1</sup>

	1. In Low Germany.	2. On the Alps.	3. Above the Limit of Trees.
Coleoptera ... ..	89·6	59·0	48·2
Diptera ... ..	305·5	324·9	334·6
Hymenoptera ... ..	525·7	242·0	136·8
(Apidæ) ... ..	(413·1)	(200·0)	(144·6)
Lepidoptera ... ..	69·8	371·5	428·3
Other Insects... ..	9·4	2·6	2·1
TOTAL ... ..	1,000·0	1,000·0	1,000·0

<sup>1</sup> Cf. *Nature*, vol. xxi. p. 275, 1880.



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*Rendiconto, etc., della R. Accad. dei*

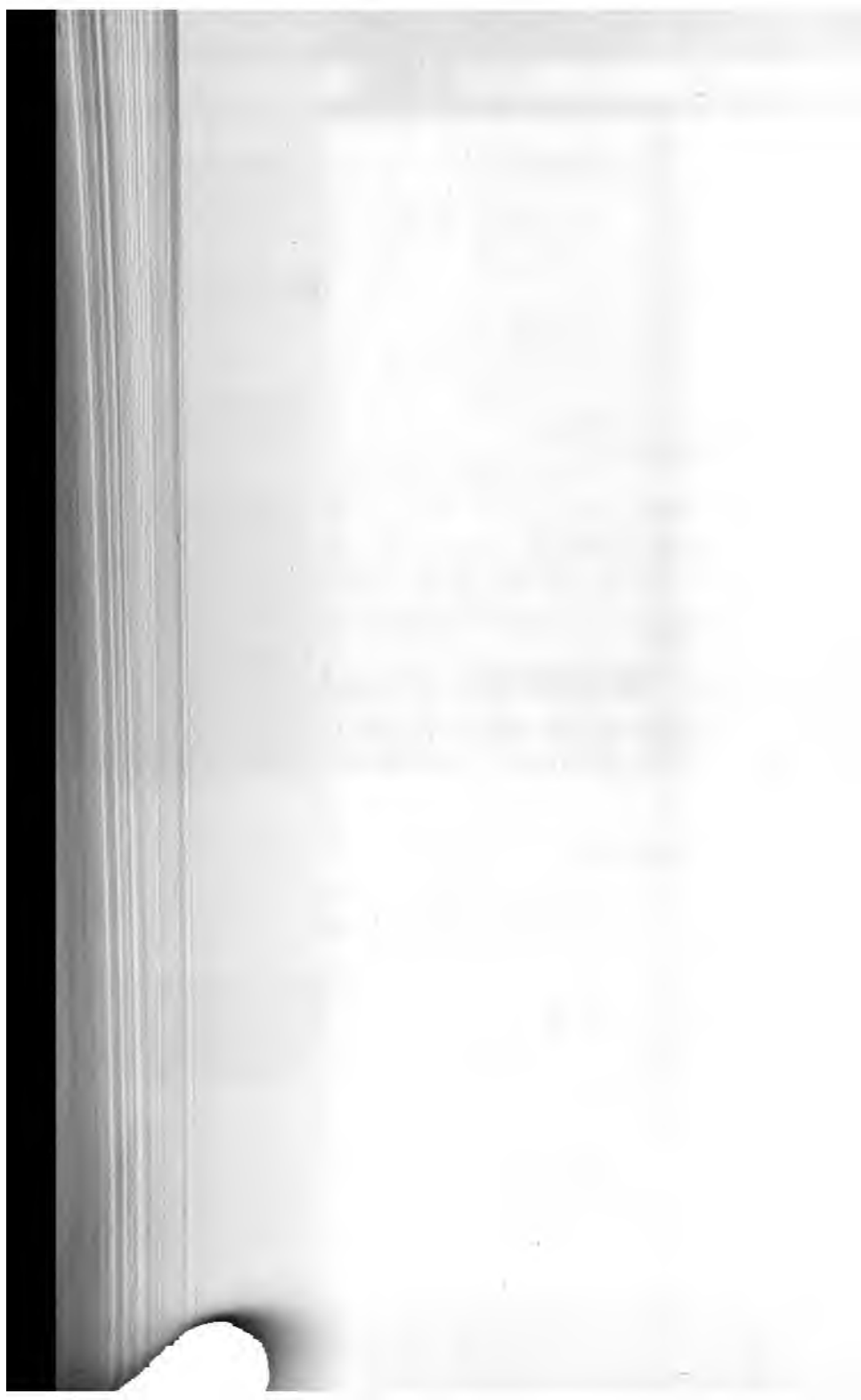
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## INDEX OF INSECTS,

### WITH REFERENCES TO THE PLANTS VISITED BY THEM.

ABBREVIATIONS.—L. = Lippstadt ; T. = Teklenburg, Herr Borgstette ; Sld. = Sauerland ; Th. = Thuringia.

Numbers placed in brackets after an insect's name, indicate the length of the insect's proboscis in millimetres.

The plants visited are designated by the numbers which they bear in the third section of this book. To facilitate reference, the first syllable of the plant's order or genus is also given.

Insects useless in the work of fertilisation are marked thus, † ; those (equally useless) which bite through or burst open the flower forcibly are marked thus, ‡. Those cases in which the insect fails to obtain the honey or pollen which it seeks are marked with an asterisk (\*).

#### I. COLEOPTERA (129 species, 469 different visits).

##### A. *Buprestidae* (1 species, 4 visits).

*Anthaxia nitidula*, L., L., Ran. 7 ; Ros. 153 ; Comp. 225, 274.

##### B. *Cerambycidae* (1 species, 80 visits).

*Clytus arietis*, L., L., Umb. 185, Ros. 152, 149, 135, 133.

— *mysticus*, L., L., Ros. 153.

*Grammoptera laevis*, F., L., List. 13 ; Corn. 197.

— *lurida*, F., L. T., Corn. 197 ; Umb. 185.

— *ruficornis*, Pz., L. T., Umb. 179, 187, 186 ; Ros. 153, 149, 138, 137.

*Leptura livida*, F., L. T., List. 380 ; Umb. 179, 188, 184 ; Ros. 135, 133 ;

*Convolv.* 311 ; Scab. 211 ; Jas. 283 ; Comp. 225, 229, 233, 227, 217, 267.

— *testacea*, L., L., Comp. 225.

*Pachyta collaris*, L., Th., Umb. 185.

— *octomaculata*, F., Sld. T. Siebengeb., Umb. 179, 181, 194, 185, 184 ; Ros.

134, 135, 130 ; Scab. 211 ; Comp. 229.

*Rhagium inquisitor*, L., Sld., Umb. 194 ; Ros. 148.

*Strangalia armata*, Hbet. (S. *calcarata*, F.), L. Sld., Corn. 197 ; Ros. 148, 135, 133 ; Scab. 211 ; Comp. 229.

— *atra*, F., L. Sld. T., Corn. 197 ; Ros. 149, 135 ; Scab. 211 ; Comp. 229.

— *attenuata*, L., L., Corn. 197 ; Ros. 149, 130, 133 ; Scab. 211 ; Comp. 229, 233.

— *bifasciata*, Müll., Th., Umb. 191, 195.

— *melanura*, L., L. Sld., Umb. 185 ; Ros. 135 ; Scab. 211 ; Comp. 253, 229, 231.

— *nigra*, L., L. Sld., Umb. 194 ; Ran. 7, Cist. 45 ; Ros. 148, 135, 133 ; Plant. 368.

*Toxotus meridianus*, L., Siebengeb., Scab. 211

##### C. *Chrysomelidae* (17 species, 32 visits).

*Adimonia sanguinea*, F., L., Ros. 152.

*Cassida murræa*, L., L., Comp. 223.

— *nebulosa*, L., L., Cruc. 33.

*Ceythra cyanea*, F., L., Ros. 153.

*Ceythrascopolina*, L., Th., Umb. 181, 191.  
*Crioceris 12punctata*, L., L., Umb. 177.  
*Cryptocephalus Moræi*, L., L., Papil. 108; Comp. 267.

— *sericeus*, L., Sld. T. Th., Umb. 194, 185; Ran. 7; Hyperic. 68; Papil. 108†; Scab. 211, 212; Jas. 283; Comp. 258, 246, 225, 237, 267.

— *vittatus*, F., Sld., Papil. 108†.

*Donacia dentata*, Hoppe, L., Nuph. 19.  
*Galeruca calmeriensis*, F., T., Umb. 182.  
*Haltica fuscicornis*, L., L., Malv. 69.

— *nemorum*, L., L., Crucif. 33.

*Helodes aucta*, F., L., Ran. 7.

— *phellandrii*, L., L., Umb. 188; Ran. 5.

*Luperus flavipes*, L., L., Ros. 148.

*Plectroscelis dentipes*, E. H., L., Crucif. 33.

#### D. *Cistelidæ* (2 species, 9 visits).

*Cistela murina*, L., L. T., Umb. 179, 185; Ran. 7; Geran. 78; Ros. 149, 133; Comp. 267.

— *rufipes*, F., L., Scroph. 324†.

#### E. *Cleridæ* (1 species, 5 visits).

*Trichodes apiarius*, L., L. T. Th., All. 392; Umb. 179, 191, 194, 174; Comp. 229.

#### F. *Coccinellidæ* (6 species, 14 visits).

*Coccinella bipunctata*, L., L., Comp. 234.

— *mutabilis*, Scrib., Th., Comp. 255.

— *14punctata*, L., L., Umb. 190; Berberid. 18; Cruc. 40; Parn. 157; Ros. 151.

— *5punctata*, L., L., Comp. 234.

— *7punctata*, L., L., Umb. 190; Parn. 157; Geran. 83; Comp. 274.

*Exochomus auritus*, Scrib., L., Umb. 194; Comp. 225.

#### G. *Cryptophagidæ* (1 species, 2 visits).

*Antherophagus pallens*, Ol., L., Sld., Digit. 256†; Camp. 278.

#### H. *Curculionidæ* (18 species, 24 visits).

*Apion columbinum*, Grm., L., Adoxa 198.

— *onopordi*, K., L., Chrysospl. 155.

— *varipes*, Grm., L., Chrysospl. 155.

— *spec.*, L., Ros. 152.

*Bruchus* sp., L., Umb. 177, 185; Comp. 248, 234.

*Ceutorhynchus pumilio*, Gylh., L., Cruc. 33.

— *sp.*, L., Cruc. 35.

*Gymnetron campanulæ*, L., Sld., Camp. 277.

— *graminis*, Gylh., Th., Camp. 282.

*Larinus Jaceæ*, L., Th., Comp. 248, 246.

— *senilis*, F., Th., Comp. 240.

*Nanophyes lythri*, F., L., Lythr. 165.

*Otiorhynchus ovatus*, L., L., Camp. 277.

— *picipes*, F., L., Corn. 197.

*Phyllobius maculicornis*, Grm., L., Ros. 152.

*Ph. oblongus*, L., L., Umb. 177.

*Rhynchites æquatna*, L., L., Ros. 151.

*Spermophagus cardui*, Schh., Th., Umb. 179, 195; Comp. 276.

#### I. *Dermostidæ* (6 species, 44 visits).

*Anthrenus claviger*, Er., L., Ros. 153, 149, 132.

— *muscorum*, L., L., Ros. 152, 133.

— *pimpinellæ*, F., L., Umb. 173, 179, 190, 194, 195, 186, 184, 174; Cruc. 38; Rhus 88; Ros. 153, 148, 149, 138, 130, 132, 133; Comp. 229.

— *scrophulariæ*, L., L., Umb. 186, 184; Ros. 148, 149, 153, 138, 132, 133.

*Attagenus pelli*, L., L., Berber. 18, Ros. 152, 153, 133.

*Byturus fumatus*, F. (including *B. tomentosus*, F.) L., Corn. 197; Ran. 7, 8; Geran. 78; Ros. 152, 134, 135, 137, 133.

#### K. *Elatridæ* (16 species, 36 visits).

*Adrastus pallens*, Er., L., Umb. 188.

*Agriotes aterrimus*, L., L., Umb. 179, Ros. 152.

— *gallicus*, Lap., Th., Umb., 195, 183; Rubiac. 206; Comp. 248, 228.

— *sputator*, L., Th., Umb. 195.

— *ustulatus*, Schall., Th., Umb. 194, 195; Comp. 248, 153.

*Athous niger*, L., L., Corn. 197; Umb. 179, 185; Comp. 229, 234.

*Cardiophorus cinereus*, Hbst., L., Ros. 133.

*Corymbites hæmatodes*, F., Siebengeb., Umb. 194.

— *holosericeus*, L., L., Umb. 194, Ros. 152; Comp. 246.

— *quercus*, Ill., L., Umb. 185.

*Diacanthus æneus*, L., L., Ros. 135.

*Dolopius marginatus*, L., L., Corn. 197; Ros. 152.

*Læon murinus*, L., L., Umb. 179, 185; Ros. 133.

*Limoni* *cylindricus*, Payk., L., Ros. 152, 135.

— *parvulus*, Pz., L., Cruc. 33; *Salix* 378; Ros. 152.

*Synaptus filiformis*, F., L., Umb. 185.

#### L. *Hydrophilidæ*.

*Cercyon anale*, Pk., L., Cruc. 33.

#### M. *Lagriidæ*.

*Lagria hirta*, L., L., Ros. 153.

*N. Lathridii.*

*Corticaria gibbosa*, Hbst., *L.*, *Chrysospl.* 155.

*O. Lamellicornia* (6 species, 39 visits).

*Cetonia aurata*, *L.*, *Sld.* Th., *Umb.* 179, 193; *Cruc.* 32; *Ros.* 152, 148, 149, 130; *Rubiace.* 206; *Sambuc.* 199; *Comp.* 229.

*Hoplia philanthus*, *Sulz.*, *Sld.*, *Umb.* 194; *Scab.* 211.

*Melolontha vulgaris*, *L.*, *L.*, *Ros.* 152, 149.

*Phyllopertha horticola*, *L.*, *L.*, *Umb.* 179; *Ros.* 148, 149, 133; *Caprif.* 200.

*Trichius fasciatus*, *L.*, *L.* *Sld.*, *Umb.* 179, 178, 187, 194, 195, 174; *Clem.* 1; *Thal.* 2; *Ros.* 135, 130, 131, 133; *Caprif.* 199; *Scab.* 211; *Comp.* 248, 246, 229, 237; *Valer.* 208.

— *nobilis*, *L.*, *L.*, *Comp.* 229.

*P. Malacodermata* (13 species, 51 visits).

*Anthocomus fasciatus*, *L.*, *L.*, *Umb.* 177, 186; *Cruc.* 34, 38; *Ros.* 148, 149; *Plant.* 362.

*Dasys tes flavipes*, *F.*, *L.*, *Umb.* 179, 181; *Cruc.* 38; *Umb.* 82; *Ros.* 138, 142, 133; *Comp.* 229.

— *pallipes*, *Pz.*, *Th.*, *Umb.* 195.

— *sp.*, *L.*, *Bry.* 171†, *Ros.* 149; *Scroph.* 323†.

*Malachius æneus*, *F.*, *L. T.*, *Umb.* 185, 186; *Geran.* 78; *Ros.* 152; *Plant.* 368; *Comp.* 229.

— *bipustulatus*, *F.*, *L. T.* *Sld.*, *Umb.* 179, 185; *Cruc.* 38; *Ros.* 135, 138, 133; *Papil.* 119†, *Comp.* 274, 260.

— *sp.*, *L.*, *Comp.* 276.

*Telephorus fuscus*, *L.*, *L.*, *Umb.* 179, 194, 185.

— *lividus*, *L.*, *L.*, *Umb.* 194, 185, 186.

— *melanurus*, *L.*, *L.* *Sld.*, *Umb.* 181, 178, 190, 194; *Comp.* 248.

— *pellucidus*, *F.*, *L.*, *Corn.* 197.

— *rusticus*, *F.*, *L.*, *Umb.* 177, 185; *Ros.* 135.

— *testaceus*, *L.*, *L.*, *Ros.* 153.

*Q. Mordellidæ* (9 species, 35 visits).

*Anaspis frontalis*, *L.*, *L.*, *Umb.* 179, 186; *Ros.* 153, 148, 133.

— *maculata*, *Fourc.*, *L.*, *Ros.* 133.

— *rufilabris*, *Gylh.*, *T.*, *Umb.* 179; *Ros.* 152.

— *ruficollis*, *F.*, *L.*, *Ros.* 149.

*Mordella abdominalis*, *F.*, *L.*, *Ros.* 153.

— *aculeata*, *L.*, *L.*, *Umb.* 179, 195; *Ran.* 7; *Ros.* 148, 149, 138, 130, 133; *Rubiace.* 206; *Caprif.* 200; *Comp.* 248, 229.

*Mordella fasciata*, *F.*, *L.*, *Umb.* 179, 178, 194, 195, 185; *Rubiace.* 206; *Comp.* 248, 229, 228, 265.

— *pumila*, *Gylh.*, *L.*, *Umb.* 185; *Ran.* 4, 7.

— *pusilla*, *Dej.*, *L.*, *Ran.* 7.

*R. Nitidulidæ* (4 species, 65 visits).

*Cychramus luteus*, *F.*, *Sld.* T., *Umb.* 179; *Ros.* 130.

*Epurea*, *sp.*, *L.*, *Umb.* 185; *Cruc.* 35; *Ros.* 152.

*Meligethes* *sp.*, *L.*, *Lil.* 394; *Cypriped.* 386\*; *Corn.* 197; *Umb.* 190, 194, 185, 186, 184, 174; *Nuph.* 19; *Ran.* 4, 7, 8, 9, 11; *Papav.* 20; *Cruc.* 30, 35, 39; *Salix* 378; *Oxalis* 75; *Cary.* 65, 63; *Lythr.* 165; *Onagr.* 167; *Ros.* 151, 152, 153, 148, 149, 135, 138, 139, 142, 136, 132, 133, 127, 128; *Papil.* 111, 112; *Convolv.* 311†; *Bor.* 300; *Scroph.* 323†; *Plant.* 368; *Caprif.* 200; *Scab.* 211; *Camp.* 278, 280; *Comp.* 229, 233, 217, 236, 263, 274; *Valer.* 209.

*Thalycra sericea*, *Er.*, *L.*, *Corn.* 197; *Umb.* 194.

*S. Œdemeridæ* (3 species, 12 visits).

*Asclera cœrulea*, *L.*, *L.*, *Ros.* 153.

*Œdemera flavescens*, *L.*, *L.* Th., *Umb.* 182.

— *virescens*, *L.*, *L. T.* Th., *Umb.* 183, 194; *Ran.* 7; *Cary.* 65; *Ros.* 135; *Convolv.* 311; *Ech.* 310; *Jas.* 283; *Comp.* 238, 217.

*T. Phalacridæ* (3 species, 4 visits).

*Olibrus æneus*, *F.*, *L.*, *Chrysospl.* 155; *Ros.* 151.

— *affinis*, *Sturm.*, *L.*, *Cary.* 67.

— *bicolor*, *F.*, *L.*, *Scab.* 211.

*U. Staphylinidæ* (2 species, 7 visits).

*Anthobium spec.*, *Sld.*, *Papil.* 112; *Camp.* 277.

*Omalium florale*, *Pk.*, *L.*, *Cruc.* 30; *Cerast.* 60; *Pulm.* 304; *Prim.* 288.

*V. Tenebrionidæ.*

*Microzoum tibiale*, *F.*, *L.*, *Ros.* 152.

II. DIPTERA (253 species, 1598 different visits).

BRACHYCERA (232 species, 1557 different visits).

*A. Asilidæ* (3 species, 3 visits).

*Dioctria atricapilla*, *Mgn.*, *T.*, *Ran.* 7.

— *Reinhardi*, *Wiedem.*, *Sld.*, *Umb.* 194.

*Isopogon brevirostris*, Fall., Sld., Umb. 181.

*B. Bombyliidae* (9 species, 57 visits).

*Anthrax flava*, Mgn., Sld. Th., Umb. 179, 175, 193, 194, 195; Rubiac. 205; Comp. 248.

— *hottentotta*, L., Sld., Comp. 237.

— *maura*, L., Th., Umb. 191, 192.

*Argyromorpha sinuata*, Fall., L. T., Cruc. 38; Hyper. 68\*.

*Bombylius canescens*, Mik., Th., Hyper. 68; Comp. 267.

— *discolor*, Mgn. (11—12), L., Coryd. 23†, 24†; Cruc. 30; Viol. 47, 48; Bor. 304; Lab. 349; Vinca, 293; Prim. 288.

— *major*, L. (10), L. T., Umb. 182; Coryd. 23†, 24†; Cruc. 30; Viol. 49; Salix 378, 379; Ros. 150; Bor. 304, 306; Lab. 362, 349; Vinca, 293; Syr. 291; Prim. 282; Comp. 236.

*Exoprosopa capucina*, F., L., Scab. 212; Jas. 282; Comp. 225.

*Systoechus sulfureus*, F., Sld. Th., Lin. 74; Malv. 72; Ros. 143; Papil. 100\*, 94†; Scroph. 317, 330; Lab. 344, 340; Rubiac. 205, 207; Camp. 277; Comp. 229, 271, 272.

*C. Conopidae* (13 species, 54 visits).

*Conops flavipes*, L. (4—5), L. Sld. T., Papil. 90†; Phlox, 299; Lab. 350; Rubiac. 206; Comp. 257, 248, 229.

— *quadrifasciatus*, Deg., L., Umb. 181.

— *scutellatus*, Mgn., Th., Comp. 246.

*Myopa buccata*, L. (4½—5), L., Salix 377, 378; Papil. 98†, 95.

— *polystigma*, Rond., L., Ros. 133; Lab. 342.

— *testacea*, L. (3½), L. Sld. Th., Salix 377; Ros. 152; Papil. 95†, 98, 108\*; Lab. 340.

— *variegata*, Mgn., L., Lab. 342.

— *sp.*, Th., Comp. 255.

*Ocemomyia atra*, F., T., Comp. 266.

*Physocephala rufipes*, F., L. Th., Ros. 135, 133; Jas. 283; Comp. 248, 246.

— *vittata*, F., L., Ech. 310; Jas. 283; Comp. 257, 225.

*Sicus ferrugineus*, L., L. Sld. T., Ros. 142; Papil. 100\*, 108\*; Lab. 340, 342; Scab. 211, 213; Jas. 283; Comp. 253, 229, 237, 266, 265, 276, 271, 272, 270, 260; Valer. 208.

*Zodion zineureum*, F., Sld., Umb. 194.

*D. Dolichopidae* (2 species, 2 visits).

*Dolichopus æneus*, Deg., L., Umb. 178.

*Gymnopternus cherophylli*, Mgn., L., Umb. 191.

*E. Empidæ* (13 species, 81 visits).

*Empis leucoptera*, Mgn., L., Hott. 289.

— *livida*, L. (2½—3, dry), L., All. 393; Orch. 386; Corn. 197; Umb. 179, 187, 194; Ran. 8; Papav. 21; Cruc. 27, 28; Hyper. 68; Lin. 74; Cary. 61; Onagr. 166; Ros. 150, 152, 153, 135, 138, 128; Papil. 117; Convolv. 311; Scroph. 326; Lab. 342, 338; Hott. 289; Scab. 211, 212; Jas. 283; Comp. 259, 248, 249, 233, 238, 217, 274, 262; Valer. 208.

— *opaca*, F. (3—3½, dry), L., Cruc. 30; Cary. 65, 60; Ros. 133; Bor. 307; Caprif. 204; Comp. 217, 274.

— *pennipes*, L., L., Hottonia 289.

— *punctata*, F., L., Cypris. 386\*; Umb. 179, 185; Ros. 133; Comp. 274.

— *rustica*, Fall., L., Umb. 187; Cary. 60; Onagr. 166; Ros. 152, 127, 128; Lab. 342, 338; Comp. 257, 229; Valer. 208.

— *stercorea*, L., L., Umb. 185.

— *tesselata*, F. (3—3½, dry), L., Umb. 182; Ran. 7; Cary. 65; Ros. 135, 133; Lab. 338; Scab. 211; Comp. 237.

— *sp.*, L., Umb. 178; Salix 378; Convolv.

*Microphorus velutinus*, Macq., L., Ros. 153.

*Rhamphomyia plumipes*, Fall., L., Camp. 277.

— *su'cata*, Fall., L., Salix 378.

*Tachydromia connexa*, Mgn., L., Ros. 153.

*F. Leptidae* (2 species, 2 visits).

*Atherix ibis*, F., L., Umb. 187.

*Leptis strigosa*, Mgn., L., Cary. 60.

*G. Muscidae* (85 species, 387 visits).

*Allophora hemiptera*, F., T., Umb. 190.

*Anthomyia æstiva*, Mgn., L., Cary. 60.

— *obelisca*, Mgn., L., Rut. 84.

— *pratensis*, Mgn., L., Rut. 84.

— *radicum*, L., L., Umb. 186; Ran. 10; Rut. 84; Ros. 151.

— *sp.*, L., Cypris. 386\*; Umb. 172, 179; Ran. 6, 7, 8, 10, 11; Berb. 18; Cruc. 30, 37; Geran. 76; Cary. 63, 55; Onagr. 170; Ros. 138, 142, 145, 130, 132, 133, 127; Plant. 96.

*Aricia incana*, Wiedem., L., Umb. 178; Comp. 238.

— *obscurata*, Mgn., L., Umb. 179.

— *serva*, Mgn., L., Ros. 153.

— *vagans*, Fall., L., Umb. 188.

*Borborus niger*, Mgn., Adoxa 198.

*Calliphora erythrocephala*, Mgn., L., Gross. 161; Umb. 194; Salix 378;

- Rhus*. 88 ; Rut. 84 ; Ros. 151 ; Scroph. 329 ; Valer. 208.  
*Calliphora vomitoria*, L., L., Umb. 178, 194, 174 ; Euon. 85 ; Valer. 208.  
*Calobata cothurnata*, Pz., L., Bor. 305.  
*Chlorops circumdata*, Mgn., L., Cary. 66.  
— sp., L., Ros. 153, 127.  
*Cyrtoneura coerulescens*, Macq., L., Ran. 7.  
— *curvipes*, Macq., L., Umb. 188, 192.  
— *simplex*, Loew, L., Umb. 176, 178, 192, 186 ; Ros. 133.  
— sp., L., Ros. 153.  
*Demoticus plebejus*, Fall., L., Comp. 270.  
*Dexia canina*, F., T., Comp. 214.  
— *rustica*, F., Th., Umb. 193.  
*Echinomyia fera*, L., L. T., Umb. 172, 179, 177, 190, 194, 185 ; Geran. 78 ; Ros. 152, 153, 134 ; Caprif. 200 ; Comp. 214.  
— *ferox*, Pz., L., Jas. 283 ; Comp. 226.  
— *grossa*, L., L., Umb. 194.  
— *magnicornis*, Zett., L. T. Th., Sed. 164 ; Umb. 194 ; Ros. 133.  
— *tesselata*, F., L., Bor. 305 ; Lab. 335 ; Scab. 317 ; Jas. 283 ; Comp. 245, 229, 227.  
*Exorista vulgaris*, Fall., L., Umb. 194, 186.  
*Gonia capitata*, Fall. (4—5), L., Comp. 225.  
*Graphomyia maculata*, Scop., L., Umb. 194, 185 ; Ros. 154.  
*Gymnosoma rotundata*, L., L. Th., Umb. 177, 191, 192, 196, 195, 186, 184 ; Lab. 133 ; Comp. 225, 228.  
*Helomyza affinis*, Mgn., L., Neottia 381.  
*Hydrotea dentipes*, F., L., Cary. 65.  
*Lucilia albiceps*, Mgn., L., Ros. 133 ; Comp. 214.  
— *casar*, L., L., Umb. 172, 178, 194.  
— *cornicina*, F., L., Umb. 173, 176, 179, 178, 188, 192, 194, 174 ; Euon. 86 ; *Rhus* 88 ; Rut. 84 ; Til. 73 ; Fagop. 369 ; Ros. 151, 142, 133 ; Lab. 340, 339, 337 ; Scab. 212 ; Comp. 248, 229, 233, 217 ; Valer. 208.  
— *sericata*, Mgn., L., Umb. 194, 185 ; Comp. 248.  
— *silvarum*, Mgn., L., Umb. 179, 178, 190, 193, 194 ; Rut. 84 ; Cary. 55 ; Ros. 142, 133 ; Lab. 339, 337 ; Comp. 229.  
— *spec.*, L., Umb. 179, 185, 195 ; Ascl. 295† ; Scab. 212 ; Comp. 222, 238.  
*Macquartia præfica*, Zett., L., Comp. 229.  
*Mesembrina meridiana*, L., L., Umb. 178, 190 ; Ros. 142, 138.  
*Micropalpus fulgens*, Mgn., L., Scab. 211.  
*Miltogramma punctata*, Mgn., L., Umb. 178, 179.  
*Musca corvina*, F., L., Umb. 178, 179, 185, 192, 194 ; Berb. 18 ; Fagop. 369 ; Cary. 66 ; Ros. 151, 138, 133 ; Bor. 305 ; Lab. 338 ; Rubiac. 205 ; Comp. 248, 229, 217.  
— *domestica*, L., L., Ran. 12 ; Berb. 18 ; Euon. 85 ; Til. 73 ; Cary. 66 ; Onagr. 170 ; Ros. 151 ; Valer. 208.  
*Myodina vibrans*, L., L., Aristol. 376.  
*Nemoreia* sp., L., Umb. 194.  
*Oecyptera brassicaria*, F., L., Umb. 178, 194 ; Lab. 340, 342 ; Ascl. 295 ; Jas. 283 ; Comp. 248.  
— *cylindrica*, F., L., Lab. 342 ; Scab. 211 ; Jas. 283 ; Comp. 248, 225, 221.  
*Oliviera lateralis*, Pz., L., Jas. 283 ; Comp. 248, 238.  
*Onesia cognata*, Mgn., L., Berb. 18 ; Ros. 139, 133.  
— *floralis*, R. D., L., Umb. 194 ; Nuph. 19 ; Berb. 18 ; Cary. 55 ; Ros. 150, 152, 153, 135, 139, 133 ; Bor. 305, 306, 307 ; Lab. 337, 338 ; Comp. 248, 238, 274 ; Valer. 207.  
— *sepulchralis*, Mgn., Th., Umb. 193, 194 ; Berb. 18 ; Ros. 153 ; Bor. 305 ; Lab. 337, 338 ; Comp. 237.  
*Phasia analis*, F., Th., Umb. 191.  
— *crassipennis*, F., Th., Umb. 191.  
*Phorocera assimilia*, Fallen, L., Umb. 194.  
*Platystoma seminationis*, F., Comp. 248.  
*Pollenia rudis*, F., L., Umb. 179 ; Ran. 12 ; Rut. 84 ; Salix 378 ; Cary. 62 ; Ros. 151 ; Comp. 222.  
— *Vespillo*, F., L., Thalic. 3 ; Parn. 157 ; Fagop. 369 ; Cary. 62 ; Ros. 151, 139 ; Bor. 305 ; Lab. 339 ; Comp. 229, 233, 238.  
*Prosenia siberita*, F., (6, dry) L., Clem. 1 ; Lab. 342.  
*Psila fimetaria*, L., L., Umb. 185.  
*Pyrellia aenea*, Zett., L., Sed. 162 ; Umb. 194 ; Comp. 229.  
— *cadaverina*, L., L., Cary. 55 ; Lab. 337.  
*Sapromyza apicalis*, Loew, L., Arist. 376.  
*Sarcophaga albiceps*, Mgn., L., Umb. 179, 177, 195 ; Rut. 84 ; Ros. 133 ; Lab. 340, 339, 337.  
— *carnaria*, L., L. Th., Umb. 172, 176, 177, 193, 194 ; Parn. 157 ; Euon. 85 ; *Rhus* 88 ; Rut. 84 ; Til. 73 ; Fagop. 369 ; Polyg. 370 ; Cary. 55 ; Ros. 153, 142, 138 ; Lab. 340, 338 ; Comp. 248, 233, 223.  
— *dissimilia*, Mgn., L., Umb. 186.  
— *hæmarrhoa*, Mgn., L., Umb. 186, 194 ; Rut. 84 ; Comp. 233.  
— *spec.*, L., Umb. 185, 190 ; Lab. 338.

- 7; *Fagopyr.* 369; *Ros.* 133; *Comp.* 270, 261.  
*Pipiza lugubris*, F., L., *Comp.* 229.  
 — *notata*, Mgn., L., *Ros.* 153.  
*Pipizella annulata*, Macq., L., *Umb.* 175, 194, 195.  
 — *virens*, F., L. T., *Umb.* 179, 177, 190, 194; *Ran.* 10.  
 — *spec.*, L., *Jas.* 283.  
*Platycheirus albianus*, F., L. T., *Ran.* 7; *Bor.* 306.  
 — *manicatus*, Mgn., L., *Cary.* 60.  
 — *peltatus*, Mgn., L., *Umb.* 177; *Geran.* 76; *Cary.* 65.  
*Pyrophæna* sp., L., *Umb.* 177.  
*Rhingia rostrata*, L. (including *campestris*, Mgn.) (11—12), L., *Lil.* 390\*; *Ir.* 387†; *Thal.* 2; *Ran.* 11; *Berb.* 18; *Papav.* 21; *Cruc.* 28, 30, 34, 35, 40; *Geran.* 76, 78, 79, 80; *Malv.* 69; *Polygon.* 370; *Cary.* 65, 62, 52\*, 57, 59\*; *Lythr.* 165; *Ros.* 150, 152, 153, 148, 134, 135, 138, 139, 145, 136, 133, 129; *Papil.* 112; *Bor.* 310, 300, 304, 305; *Solan.* 313; *Scroph.* 318, 324; *Lab.* 366, 359†, 361\*, 352, 353, 349; *Ol.* 291; *Plant.* 368; *Hott.* 289; *Eric.* 285; *Caprif.* 202, 203, 204; *Scab.* 211, 212; *Camp.* 279; *Comp.* 257, 259, 217, 274; *Valer.* 209 (67 visits).  
*Serycomyia borealis*, Fall., T. Th., *Eric.* 287.  
 — *lappona*, L., *Sld.*, *Comp.* 272.  
*Syrilla pipiens*, L., L. Sld. Th., *Alism.* 398; *Gross.* 158, 161; *Umb.* 176, 179, 177, 178, 175, 187, 188, 190, 192, 193, 194, 195, 185, 186, 184; *Clem.* 1; *Thal.* 3; *Ran.* 6, 7; *Papav.* 21; *Cruc.* 27, 28, 37, 38; *Res.* 42; *Parn.* 157; *Viol.* 46; *Salix* 378; *Euon.* 85; *Rhus* 88; *Rut.* 84; *Geran.* 80; *Polygon.* 369, 370\*, 371, 372, 373, 374; *Cary.* 66, 60, 61, 63, 55; *Lythr.* 165; *Ros.* 151, 148, 149, 135, 138, 139, 142, 145, 130, 131, 133; *Bor.* 305; *Solan.* 312, 313; *Scroph.* 317, 319, 325, 326; *Lab.* 340, 339, 337, 338; *Ol.* 291; *Prim.* 290; *Eric.* 287; *Rubi.* 205; *Jas.* 283; *Comp.* 248, 225, 229, 233, 227, 228, 234, 238, 220, 216, 217, 263, 260; *Valer.* 207 (89 visits).  
*Syrphus arcuatus*, Fall., L. T., *Umb.* 177; *Ros.* 140; *Bor.* 310; *Comp.* 265, 275.  
 — *balteatus*, Deg. (2), L. T., *Papav.* 21; *Cruc.* 37; *Parn.* 157; *Salix* 378; *Hyper.* 68; *Geran.* 78; *Cary.* 55; *Convolv.* 311; *Plant.* 368; *Camp.* 278; *Comp.* 266, 265, 275, 262, 271, 273.  
 — *corollæ*, F., L., *Umb.* 185; *Comp.* 229.  
 — *decorus*, Mgn., T., *Cruc.* 35.  
 — *excisus*, Zett., L., *Parn.* 157; *Ros.* 133.  
 — *glaucius*, L., L., *Umb.* 194.  
 — *nitidicollis*, Mgn., (3), L. T., *Umb.* 179, 181; *Rut.* 84; *Ros.* 179; *Convolv.* 311; *Comp.* 229, 274, 271.  
*Syrphus ochrostoma*, Zett., L., *Caprif.* 202.  
 — *pyrastri*, L., L. T., *Umb.* 179, 177, 181, 192, 194, 195; *Clem.* 1; *Parn.* 157; *Cist.* 45; *Salix* 378; *Geran.* 78; *Fagopyr.* 369; *Cary.* 57; *Ros.* 150; *Bor.* 310; *Lab.* 338; *Scab.* 212; *Jas.* 283; *Comp.* 224, 274, 271.  
 — *ribesii*, L. (3—4), L. T., *Umb.* 179, 177, 178, 194, 185; *Ran.* 7; *Parn.* 157; *Cist.* 45; *Salix* 378; *Hyper.* 68; *Euon.* 85; *Rut.* 84; *Geran.* 78; *Polygon.* 370; *Cary.* 65; *Onagr.* 166; *Ros.* 133; *Plant.* 367; *Rubi.* 205; *Scab.* 311; *Comp.* 224, 234, 237, 265.  
 — *umbellatarum*, Mgn., *Sld.*, *Comp.* 237.  
 — *spec.*, L., *Cruc.* 27; *Cary.* 60; *Ros.* 138, 139; *Scroph.* 330; *Eric.* 287; *Comp.* 248, 263.  
*Tropidia milesiformis*, Fall., L.,  
*Volucella bombylans*, L. (7—8), L. Sld. T., *Orch.* 390; *Polyg.* 370; *Cary.* 64; *Ros.* 147, 130; *Pap.* 98, 100\*; *Lab.* 350; *Eric.* 286; *Scab.* 211; *Jas.* 283; *Comp.* 253, 225, 237, 271; *Valer.* 208.  
 — *hemarrhoidalis*, Zett., L., *Eric.* 286.  
 — *pellucens*, L., L. T. Sld., *Umb.* 178; *Cruc.* 34; *Til.* 73; *Ros.* 134, 135; *Plant.* 367; *Samb.* 199; *Scab.* 211; *Comp.* 225, 229, 237, 270.  
 — *plumata*, L., L., *Cary.* 57; *Lythr.* 165; *Ros.* 133; *Pap.* 116; *Eric.* 286; *Scab.* 211.  
*Xanthogramma citrofasciata*, Deg., L., *Umb.* 176; *Euon.* 85; *Ros.* 144.  
*Xylota femorata*, L., T., *Umb.* 182.  
 — *florum*, F., *Sld.*, *Umb.* 194.  
 — *ignava*, Pz., L., *Clem.* 1; *Ros.* 133.  
 — *lenta*, Pz., L., *Clem.* 1; *Ros.* 133.  
 — *segnis*, L., L., *Ros.* 153, 133; *Ol.* 291\*, *Caprif.* 202.  
 — *silvarum*, L., *Sld.*, *Lab.* 352\*.  
  
 K. *Tabanidæ* (4 species, 9 visits).  
*Chrysops cæcutiens*, L., L., *Umb.* 181; *Cary.* 55; *Ros.* 142; *Lab.* 285.  
*Tabanus luridus*, Pz., L., *Valer.* 208.  
 — *micans*, Mgn., L., *Umb.* 181.  
 — *rusticus*, L., L., *Sld.* Th., *Umb.* 194; *Comp.* 248, 225.  
  
 L. *Therevidæ* (1 species, 1 visit).  
*Thereva anilis*, L., L., *Umb.* 179.  
  
 NEMATOCERA (22 species, 41 visits).  
 M. *Bibionidæ* (5 species, 12 visits).  
*Bibio hortulanus*, F., L. T., *Umb.* 177, 185, 186; *Euon.* 85; *Ros.* 133.  
 — *Johannis*, L., L., *Salix* 378.

Bibio Marci, L. L., Salix 378; Ros. 153, 127.  
 Dilophus vulgaris, Mgn., L., Ros. 150, 152, 153.  
 Scatopse soluta, Loew, L., Aristol. 375.

N. *Cecidomyiidae* (2 visits).

Undetermined: Adoxa 314; Chrysospl. 155.

O. *Chironomidae* (3 species, 4 visits).

Ceratopogon sp., L., Aristol. 375; Ros. 133.  
 Chironomus sp., L., Aristol. 375.  
 Undetermined genus, Chrysospl. 155.

P. *Culicidae* (1 species, 1 visit).

Culex pipiens, L., L., Rhamn. 86.

Q. *Mycetophilidae* (5 visits).

Undetermined: Adoxa 314; Chrysospl. 155.  
 Platycera sp., L., Umb. 194.  
 Sciara Thomæ, L., L. Th., Umb. 172; Comp. 238.

R. *Psychodidae* (1 species, 1 visit).

Psychoda phalænoides, L., L., Arum 391.

S. *Simuliidae* (2 visits).

Simulia spec., Adoxa 198; Chrysospl. 155.

T. *Tipulidae* (5 species, 13 visits).

Tipula oleracea, L., L., Parn. 157; Ros. 135.  
 — spec., L., Umb. 177, 192; Valer. 390.  
 Pachyrrhina crocata, L., L. Sld. T., Umb. 179, 181, 185; Rubiac. 205.  
 — historio, F., L., Umb. 179, 194.  
 — pratensis, L., L., Umb. 185; Ros. 133.

III. HEMIPTERA (6 species, 15 visits).

Anthocoris sp., L., Umb. 178; Salix 378.  
 Capsus sp., L. Th., Umb. 194; Lythr. 165; Papil. 91†; Comp. 258, 255, 231, 228, 238.  
 Nabis sp., L., Convolv. 311†.  
 Pyrocoris aptera, L. (4), L., Comp. 274.  
 Tetyra nigrolineata, L., Th., Umb. 195.  
 Undetermined genus, L., Umb. 194; Comp. 234.

IV. HYMENOPTERA (368 species, 2,750 different visits).

A. *Apidae* (205 species, 2,191 different visits).

*Andrena* (51 species, 219 different visits).

*Andrena albicans*, K. (2—2½), L. T., Cypr. 386; Grossa. 158, 161; Umb. 179, 177; Clem. 1; Ran. 4, 7, 9, 11; Berber. 18; Coryd. 22†; Cruc. 34; Viol. 46\*; Salix 378, 379; Rhus 88; Polygon. 370; Cary. 66, 60; Ros. 150, 151, 152, 153, 148, 149, 139, 133, 127, 129; Papil. 111; Myos. 305, 306; Lab. 359†, 349\*; Caprif. 203\*; Comp. 225, 274; Valer. 209.

— albicrus, K. (3), L., Umb. 173, 179; Ran. 6; Cruc. 29; Salix 378; Fagop. 369; Cary. 66; Ros. 152, 134, 135, 139, 140, 133; Papil. 108\*; Ech. 310; Comp. 274.

— apicata, Sm., L., Sal. 378.

— argentata, Sm. = gracilis, Schenck (2—2½), L., Cary. 60; Salix 378; Ros. 139; Jas. 283; Comp. 225, 274.

— atriceps, K. = tibialis, K. (3½), L., Cypr. 12; Salix 378; Ros. 152, 153; Papil. 111; Eric. 285; Comp. 274.

— bicolor, F. = aestiva, Sm., L., Fagop. 369.

— Cetii, Schr. (3½), L., Scab. 212.

— chrysosceles, K., L., Salix 378; Ros. 153, 139; Comp. 225.

— cineraria, L., (4), L., Salix 378; Cary. 65; Comp. 274.

— cingulata, F., L., Sed. 162; Ran. 8; Comp. 274.

— coitana, K., Sld. Th., Umb. 194; Hyper. 68; Geran. 178; Malv. 72; Ros. 130; Scroph. 323†; Lab. 356; Camp. 277, 276; Jas. 283; Comp. 253, 268, 272.

— Collinsonana, K. = proxima, K., L., Umb. 179, 185, 184; Salix 378; Ros. 151; Comp. 274.

— convexiuscula, K., L., Ros. 152; Papil. 98, 95, 119; Scab. 212; Comp. 274.

— denticulata, K. = Listerella, K., L. Sld. T. Th., Ros., 143; Papil. 94; Lysim. 290\*; Comp. 225, 234, 238, 215, 268, 263, 264, 265, 273, 270.

— dorsata, K. (3), L. T., Umb. 179, 192; Papav. 20; Cruc. 30, 36; Salix 378; Hyper. 68; Geran. 76, 78; Polygon. 369, 371; Cary. 66; Ros. 152, 153, 149, 138, 139, 133, 127; Papil. 104, 96; Scroph. 318; Eric. 287; Jas. 283; Comp. 248, 225, 263, 265, 274.

— eximia, Sm. (3½), L., Salix 377.

— fasciata, Wesm. (3—4), L., Ros. 127; Papil. 100\*; Myos. 306; Comp. 274.

Geran. 78; Jas. 283; Comp. 267, 268,  
 273, 270.  
 — *fulvescens*, Sm., L. Sld., Umb. 181;  
 Ran. 10; Pap. 108\*; Comp. 267, 268,  
 263, 274, 272, 273, 269, 270.  
 — *fulvius*, K. (3—3½), L. Th., Cypr.  
 386; Umb. 177; Ran. 4, 7; Berb. 18;  
 Papav. 20; Cruc. 39; Cist. 171; Bry.  
 45; Salix. 378; Geran. 76; Malv. 69;  
 Fagop. 369; Ros. 163, 139, 133, 127;  
 Papil. 98, 100\*, 94, 108, 110, 112;  
 Scroph. 324; Lab. 349; Eric. 287;  
 Camp. 278; Jas. 283; Comp. 248,  
 225, 227, 234, 238, 236, 264, 274, 271,  
 273, 260.  
 — *fuscipes*, K. = *pubescens*, K., L. T.,  
 Eric. 287; Jas. 283; Comp. 225.  
 — *Gwynana*, K. (2½), L. Sld. T. Th.,  
 Gross. 158, 161; Clem. 1; Ran. 9;  
 Cruc. 30, 39; Salix. 378, 379; Geran.  
 78, 80; Malv. 69; Fagop. 66; Cary.  
 369; Ros. 151, 153, 135, 127; Scroph.  
 320, 324; Prim. 288; Eric. 285;  
 Scab. 211; Camp. 277, 278, 279, 281;  
 Comp. 248, 253, 237, 236, 274.  
 — *Hattorfiana*, F. (5½—7), L. Sld. Th.,  
 Cary. 53; Scab. 211; Jas. 283.  
 — *helvola*, L. (including *varians*, Rossi,  
 and *mixta*, Schenck), L., Umb. 179;  
 Berb. 18; Salix. 378; Fagop. 369;  
 Ros. 153, 136\*, 133; Jas. 283; Comp.  
 274.  
 — *labialis*, K., L. Th., Papil. 90, 119\*,  
 116; Ech. 310; Lab. 366.  
 — *lepidula*, Schenck., L., Umb. 174,  
 Comp. 225.  
 — *minutula*, K., L., Umb. 177, 191;  
 Comp. 227.  
 — *nana*, K., L., Gross. 158, 160;  
 Umb. 177, 194, 195; Cruc. 39, 40;  
 Salix. 378; Fagop. 369; Ros. 139,  
 140; Comp. 248, 225, 227.  
 — *nigroscnea*, K. (3½—4), L. Sld.,  
 Cypr. 12; Umb. 177; Cruc. 39; Res.  
 43; Bry. 171; Salix. 378; Ros. 134,  
 133, 132, 131, 130, 129, 128, 127, 126, 125, 124, 123, 122, 121, 120, 119, 118, 117, 116, 115, 114, 113, 112, 111, 110, 109, 108, 107, 106, 105, 104, 103, 102, 101, 100, 99, 98, 97, 96, 95, 94, 93, 92, 91, 90, 89, 88, 87, 86, 85, 84, 83, 82, 81, 80, 79, 78, 77, 76, 75, 74, 73, 72, 71, 70, 69, 68, 67, 66, 65, 64, 63, 62, 61, 60, 59, 58, 57, 56, 55, 54, 53, 52, 51, 50, 49, 48, 47, 46, 45, 44, 43, 42, 41, 40, 39, 38, 37, 36, 35, 34, 33, 32, 31, 30, 29, 28, 27, 26, 25, 24, 23, 22, 21, 20, 19, 18, 17, 16, 15, 14, 13, 12, 11, 10, 9, 8, 7, 6, 5, 4, 3, 2, 1, 0.

- Umb. 172, 179, 194, 185, 186; Clem. 1; Thal. 2, 3; Anem. 4; Ran. 5, 7, 9, 11, 12; Ag. 13†; Berb. 18; Diel. 22†; Coryd. 23†, 24†; Fum. 26; Cruc. 27, 29, 30, 31, 34, 35, 39, 40, 41; Res. 42, 43; Viol. 47; Cist. 51; Bry. 170†; Salix 378, 379; Rhamn. 86; Aesc. 87; Polygal. 45; Rhus. 88, 89; Rut. 84; Geran. 77, 80, 83; Lin. 75; Til. 73; Malv. 69, 70, 71, 72; Polygon. 369, 370; Cary. 65, 62, 57; Lythr. 165; Onagr. 166, 169; Ros. 150, 151, 152, 153, 148, 134, 135, 138, 139, 142, 136†, 130, 133, 127, 129; Papil. 90, 98, 100†, 101, 103, 105, 96, 97, 93†, 94, 95, 92, 111, 108, 109, 110, 111, 107, 121, 122, 117, 118†, 119†, 114, 116; Convolv. 311; Ech. 310; Bor. 301, 300†, 302, 306; Solan. 314, 315; Scroph. 318, 319, 320, 324, 325, 327, 332, 330, 335†; Lat. 366, 364, 359†, 362, 363, 360†, 355, 349†, 347, 348, 344, 340, 342; Ascl. 295; Ol. 291; Plant. 367; Prim. 288\*; Eric. 286†, 287, 284, 285; Rubiac. 207; Caprif. 201, 202, 203, 204; Scab. 211, 212, 213; Camp. 277, 278, 279; Jas. 283; Comp. 257, 258, 259, 248, 249, 250, 253, 244, 227, 234, 237, 238, 215, 217, 236, 214, 266, 263, 274, 276, 271, 270, 260; Valer. 208, 209.
- Bombus* (17 species, 509 visits).
- Bombus agrorum*, F. (= *muscorum*, L.), (10—15), L. T., Sld. Th., Smil. 390; Ir. 387; List. 380†; Orch. 382; Sed. 164; Aq. 13; Papav. 21; Coryd. 25; Viol. 48; Hyperic. 68; Rhamn. 86; Til. 73; Malv. 69, 70; Cary. 57; Lythr. 165; Onagr. 166, 169; Ros. 150, 148, 135; Papil. 90, 100, 104, 120, 117, 118, 116; Ech. 310, 300, 302, 304; Solan. 315; Scroph. 317, 321, 322, 323, 330, 335, 333; Lab. 365, 360, 356, 357, 358, 352, 353, 349; Gent. 296; Vinc. 293, 294; Eric. 286, 284, 285; Symphor. 201; Dips. 210, 211, 212; Comp. 241, 257, 258, 249, 245, 243, 244, 256 (68 visits).
- *Barbutellus*, K. (*Apathus*?) (12), L. Sld. Papil. 100; Ech. 310; Scroph. 326, 334; Lab. 349; Scab. 211; Comp. 274, 272 (9 visits).
- *campestris*, Pz. (*Apathus*) (10—12), L. T., Orch. 382; Sed. 154; Onagr. 166; Ros. 135, 100, 116; Ech. 310; Eric. 285; Scab. 211; Comp. 256, 250, 244, 238, 215 (14 visits).
- *confusus*, Schenck (12—14), L. Th., Orch. 382, 383, 384; Onagr. 165; Ros. 136; Papil. 100, 119, 116; Lab. 366, 349; Prim. 288; Eric. 285; Comp. 241, 258, 274, 273 (16 visits).
- Bombus fragrans*, Kirby<sup>1</sup> (15), L., Orch. 384; Salix 378; Ros. 136; Pap. 100 (4 visits).
- *hortorum*, L.<sup>2</sup> (18—21), L. Sld. Th., Colch. 395; Smil. 390; Ir. 387; Orch. 382, 383, 384; Berg. 156; Aq. 13; Delph. 14, 15; Aconit. 17; Diel. 22; Viol. 47; Salix 378; Malv. 69; Pom. 150; Ros. 134, 135, 136, 129; Pap. 91, 125, 117, 119; Ech. 310; Bor. 304; Scroph. 319, 320, 321, 323, 334, 335, 333; Lab. 366, 359, 361, 362, 360, 352, 349; Vinc. 293; Ol. 291; Prim. 288; Eric. 285; Scab. 211; Jas. 283; Comp. 248, 247 (49 visits).
- *hypuorum*, L. (10—12), L. Sld. T. Th., Ros. 136; Ech. 310; Scroph. 334, 365, 364; Ascl. 295; Scab. 211 (7 visits).
- *lapidarius*, L. (8—14), L. Sld. T. Th., Orch. 382, 383, 384; Sed. 164; Viol. 46, 47, 49; Salix 378; Aesc. 87; Polygal. 51; Malv. 69; Fagop. 369; Cary. 57; Onagr. 166, 169; Ros. 150, 136, 129; Papil. 100, 101, 92, 111, 112, 107, 118, 119; Ech. 310; Bor. 300†, 302, 304; Scroph. 321, 332, 333; Lab. 366, 364, 359, 358, 355, 349; Vinc. 293; Ol. 291; Prim. 288; Eric. 284; Dips. 210, 211, 212, 213; Camp. 277, 279; Comp. 240, 241, 242, 257, 258, 255, 248, 250, 251, 257, 245, 246, 238, 266, 274, 271, 270 (65 visits).
- *muscorum*, F. (= *senilis*, F. Smith) (10—14), L. T. Th., Orch. 382 (?), 383, 384; Cist. 45; Papil. 100, 102, 94, 91, 116; Ech. 310; Bor. 302; Scroph. 318, 331; Lab. 366, 364; Rubiac. 207; Caprifol. 201, 204; Comp. 240, 241, 258, 246, 274 (23 visits).
- *pratensis*, L. (8—12), L. Sld., All. 392; Orch. 382, 383, 384; Gross. 162; Berb. 18; Chelid. 21; Dicyl. 22†; Salix 378; Onagr. 166; Ros. 134, 135, 136; Papil. 98, 100†, 123, 116; Ech. 310; Bor. 301, 300†, 302, 304, 315; Scroph. 330, 334†, 335†, 364; Lab. 366, 359, 362, 363, 360, 352, 355, 349, 341; Plant. 367; Eric. 285; Caprif. 201, 204; Scab. 211, 212; Camp. 277; Comp. 257, 253, 246, 247, 237, 238, 272, 208 (52 visits).
- *Rajellus*, Ill. (10—13), L., Ir. 387; Sed. 162; Papav. 21; Diel. 22†; Viol. 47; Cary. 57; Papil. 100, 101, 117, 118; Ech. 310; Bor. 300, 304;

<sup>1</sup> Dr. Kriechbaumer tells me that the name *Pethysus* is older than *Apathus*, and *P. saltuum*, Fz., older than *Barbutellus*, K.

<sup>2</sup> According to Dr. Kriechbaumer, *B. fragrans*, K., is quite distinct from *B. fragrans*, Pall., a Siberian species. The latter must be called *B. distinguendus*, Moraw. and is, perhaps, identical with *B. elegans*, Seidl.

<sup>3</sup> Including *B. ruderatus*, F.

- Scroph. 334; Lab. 364, 359, 361†, 363, 360, 349; Eric. 286; Scab. 211; Comp. 253, 268 (23 visits).
- Bombus rupestris*, F. (Apathus) (11—14), L. T. Th., Papil. 100, 116; Ech. 310; Lab. 364, 349; Dips. 310, 211, 212; Jas. 283; Comp. 241, 257, 258, 255, 215 (14 visits).
- *Scrimahiranus*, K. (10), L. T. Th., Gross. 161; Salix 378; Ros. 135, 136, 133; Papil. 117, 116; Scroph. 319, 334, 333†, 358, 355; Eric. 284 (13 visits).
- *senilis*, F. Smith (= *B. muscorum*, F.) (11—15), L., Orch. 383; Ros. 136, 133; Papil. 100, 119, 116; Bor. 304; Scroph. 334, 359; Gent. 296; Eric. 286; Scab. 212 (12 visits).
- *silvarum*, L. (9—14), Fig. 15, L. T. Th., Orch. 383; Sed. 164; Malv. 69; Lythr. 165; Onagr. 169; Ros. 134, 135, 136, 100; Papil. 91, 118, 119, 116; Ech. 310; Bor. 300, 302, 304; Scroph. 321, 332, 334, 333; Lab. 366, 364, 359, 360, 356, 358, 353, 355, 349, 346, 347; Gent. 297; Prim. 288; Eric. 286, 285; Scab. 211, 212; Jas. 283; Comp. 240, 241, 257, 258, 259, 246, 244, 268, 274 (48 visits).
- *terrestris*, including *lucorum*, L. (7—9), L. Sld. T. Th., Lil. 394, 393; Orch. 382, 384; Gross. 161; Umb. 194; Clem. 1; Ran. 5, 8, 11; Aq. 13†; Berb. 18; Diel. 22†; Coryd. 23†, 24†; Cruc. 30; Sal. 378, 379; Hyper. 68; Esc. 87; Polygal. 51; Cary. 57; Lythr. 165; Onagr. 166; Ros. 150, 151, 135, 136†, 133, 128; Papil. 90, 100†, 92, 111, 108, 112, 118†, 119†, 115; Ech. 310; Bor. 300†, 304; Scroph. 317, 320, 321, 323, 334†, 335†, 333†; Lab. 359†, 361†, 360†, 356†, 353, 355, 349†, 342; Ascl. 295; Vinc. 293; Ol. 291; Plant. 368; Prim. 288†; Eric. 286, 287, 284, 285; Scab. 211, 212; Comp. 241, 242, 258, 255, 250, 229, 239, 215, 268, 274 (79 visits).
- *vestalis*, Fourer. (Apathus) (12), L. Sld. T. Th., Ir. 387; Ros. 135; Papil. 100, 117; Ech. 310; Scroph. 326; Lab. 349; Vinc. 293; Eric. 285; Scab. 211, 212; Comp. 253, 247, 214, 274 (15 visits).
- Ceratina cerulea*, Vill. (4—5), L., Ech. 310; Jas. 283; Comp. 267.
- Chalicodoma muraria*, F. (10), Th., Papil. 116.
- Chelostoma* (3 species, 25 visits).
- Chelostoma campanularum*, K. (3—3½), L. Sld. T. Th., Malv. 69; Lab. 347†;
- *Camp.* 277, 278, 279, 280; Jas. 283; Comp. 246, 263.
- Chelostoma florissomne*, L. = *maxillosum*, L. (3½—4), L. Th., Ran. 7, 8; Camp. 280; Comp. 274.
- *nigricorne*, Nyl. (4—4½), L. T. Sld. Th., Geran. 77, 78; Malv. 69, 72; Ech. 310; Lab. 336; Camp. 277, 278, 279, 280, 281; Comp. 225.
- Cilissa* (3 species, 16 visits).
- Cilissa hamarrhoidalis*, F. (3—4), L. Sld., Malv. 69, 71; Lab. 355; Comp. 277, 278, 279.
- *leporina*, Pz. = *tricincta*, K. (3½), L. Th., Sed. 162; Papil. 100, 101, 94, 92; Jas. 283; Comp. 248, 246.
- *melanura*, Nyl. (3—4), L. Sld. T., Lythr. 165; Comp. 273.
- Celioxys* (6 species, 28 visits).
- Celioxys acuminata*, Nyl., Th., Comp. 242.
- *spec.*, L., Ros. 140; Papil. 90; Lab. 349, 341; Ascl. 295; Comp. 211.
- *conoidea*, Ill. = *punctata*, Lep. (6), L. Th., Papil. 116; Ech. 310; Lab. 336; Scab. 211; Jas. 283; Comp. 255, 266.
- *quadridentata*, L. = *conica*, L. = *acuta*, Nyl., L., Papil. 96; Ech. 310; Scab. 211; Jas. 283; Comp. 242.
- *simplex*, Nyl. (4½), L., Bry. 171; Malv. 69; Ech. 310; Jas. 283; Comp. 218, 266.
- *umbrina*, Sm. = *parvula*, Schenck, L. Th., Ros. 135; Ech. 310; Lab. 336.
- Colletes* (4 species, 16 visits).
- Colletes cunicularia*, L. (3½—4), L., Salix 377; Eric. 285.
- *Daviesiana*, K. (2½), L. Sld., Onagr. 169; Papil. 108; Comp. 225, 229, 227, 234, 274, 270.
- *fodiens*, K. (2½), L., Papil. 100; Comp. 225, 234.
- *marginata*, L. (2), L., Papil. 101; Jas. 283; Comp. 227.
- Crocisa scutellaris*, Pz. (7—7½), T. Th., Lab. 336.
- Dasypoda hirtipes*, F. (4½—5), Fig. 10, 1., L. Th., Jas. 283; Comp. 248, 246, 266, 263 (7 visits).
- Diphysis serratula*, Pz. (7—8), L. Sld. T., Ros. 135; Papil. 90, 100, 101, 108\*, 120, 265, 271, 117; Ech. 310; Eric. 287; Scab. 211; Jas. 283; Comp. 257, 267, 271, 270 (15 visits).
- Epeolus variegatus*, L. (13½), L., Jas. 283; Comp. 248.
- Eucera longicornis*, L. (10—12), L. Sld., Orch. 383, 384; Ros. 153; Papil. 90,

\* I only lately became aware of the identity of these species; I have placed the darker varieties under *B. muscorum*, F., the light-yellow ones under *B. senilis*, Smith.

- 100, 123, 126, 117, 116; Ech. 310; Bor. 300; Lab. 359; Ol. 291; Plant. 368; Caprif. 201 (15 visits).  
*Halictoides dentiventris*, Nyl. (2—2½), L. Sld., Camp. 277, 278.
- Halictus* (32 species, 440 visits, 181 being to *Compositae*).
- Halictus albipes*, F. = *obovatus*, K. (including *affinis*, Schenck), L. Sld. Th., Umb. 179, 177, 195; Ran. 9; Salix. 378; Geran. 76; Malv. 69; Polygon. 371; Ros. 135, 133, 127; Papil. 103, 108, 116; Ech. 310; Scroph. 326, 328; Lab. 342; Ol. 291\*; Plant. 368; Scab. 211; Camp. 279; Jas. 283; Comp. 257, 248, 246, 229, 238, 223, 220, 221, 263, 274, 262, 271, 272, 260 (37 visits).
- *brevicornis*, Schenck, Th., Comp. 270.
- *cylindricus*, F. = *fulvoincinctus*, K. = *malachurus*, K. (3—4), L. Sld. T. Th., Lil. 393; Umb. 172, 179, 194; Ran. 4, 6, 7, 9, 10; Papav. 20, 21; Cruc. 30, 39; Salix 378; Geran. 76, 77, 78; Lin. 75; Malv. 71; Cary. 65; Lythr. 165; Ros. 153, 135, 139, 127; Papil. 103, 110; Ech. 310; Solan. 316; Scroph. 319, 323†, Lab. 362\*, 363\*, 342, 338; Ascl. 395; Plant. 368; Eric. 285; Scab. 211, 212; Camp. 278; Jas. 283; Comp. 241, 242, 257, 248, 253, 245, 246, 247, 225, 229, 238, 223, 220, 221, 217, 268, 263, 265, 274, 262, 271, 272, 273, 269, 270 (65 visits).
- *fasciatus*, Nyl., L., Jas. 283.
- *flavipes*, F., = *seladonius*, F. (2½), L. Th., Umb. 194; Ran. 6, 7; Papav. 20; Geran. 76; Ros. 139, 141, 133; Pap. 90, 100, 105, 95, 116; Scroph. 322; Eric. 285; Camp. 280; Jas. 283; Comp. 248, 220, 221, 263, 274, 276, 273, 270 (26 visits).
- *fulvicornis*, K., L., Umb. 195.
- *interruptus*, Pz., Th., Umb. 175, 195; Comp. 257, 246 (4 visits).
- *leucopus*, K., L. Sld. T. Th., Umb. 194; Cruc. 34; Ros. 139; Scroph. 328; Lab. 362\*; Comp. 220, 274, 271 (9 visits).
- *leucozonius*, Schr. (4), L. Sld. T. Th., Orch. 384; Umb. 191; Ran. 7; Aq. 13; Cruc. 40; Geran. 77; Ros. 135, 140; Scab. 211, 212; Jas. 283; Comp. 257, 246, 225, 229, 220, 266, 267, 263, 262, 271, 272, 273, 270 (24 visits).
- *longulus*, Sm. = *pauillus*, Schenck, L. Th., Umb. 172, 189; Ran. 7; Papav. 20; Geran. 76, 77; Convolv. 311; Scroph. 324; Lab. 338; Comp. 257, 248, 246, 243, 244, 223, 220, 263, 274, 262, 271, 260 (21 visits).
- *lucidulus*, Schenck, L., Cruc. 38; Geran. 77; Ros. 135, 138; Lab. 349\*; Jas. 283; Comp. 257, 246, 227, 274 (10 visits).
- *lucidus*, Schenck, L., Ran. 9; Ros. 134.
- *lugubris*, K. = *laevigatus*, K., L. Th., Papil. 116; Lab. 359; Comp. 263, 276, 273, 270 (6 visits).
- *maculatus*, Sm., L. T. Th., Umb. 177, 182; Ran. 7; Papav. 20; Geran. 77, 78, 79; Malv. 69; Ros. 140; Papil. 98; Lab. 338; Camp. 279; Comp. 257, 253, 248, 246, 225, 229, 228, 234, 238, 223, 220, 263, 274, 262, 271, 273 (28 visits).
- *minutissimus*, K., L., Lythr. 165; Comp. 217, 274.
- *minutus*, K. (2), L. T., Umb. 178; Comp. 257, 248, 246, 265, 262 (6 visits).
- *morio*, F. (2), L. Th., Malv. 69, 70; Cary. 56; Convolv. 311†, Scroph. 321; Lab. 346†; Comp. 225, 220, 273 (9 visits).
- *nitidiusculus*, K., L. Th., Gross. 158; Ran. 7, 9; Cruc. 27, 38; Geran. 76; Ros. 134; Convolv. 311; Ech. 310; Scroph. 328; Lab. 346†, 338; Comp. 257, 248, 246, 227, 221, 274, 262, 269, 260 (21 visits).
- *nitidus*, Schenck, L. Th., Gross. 158; Ros. 148; Ech. 310; Lab. 346†, 347, 342; Comp. 238, 223, 236, 267, 263, 274 (12 visits).
- *quadricinctus*, F.,<sup>1</sup> L. Th., Umb. 191; Ran. 7; Papil. 101, 94; Ascl. 295; Comp. 240, 241, 242, 257, 258, 225, 246, 220, 263, 264, 276, 262, 260 (18 visits).
- *quadrinotatus*, K., Th., Comp. 246.
- *quadristrigatus*, Latr.,<sup>1</sup> (5—7), Th., Comp. 255.
- *rubicundus*, Chr. (3—4½), L. Th. Gross. 161; Ran. 7; Berb. 18; Esc. 87; Ros. 151, 152; Papil. 90, 108; Eric. 286; Scab. 212; Comp. 240, 257, 248, 246, 225, 229, 263, 264, 274, 276, 262, 270, 260 (23 visits).
- *Scabiosæ*, Ill., Freiburg, Hild., Ascl. 295.
- *sexnotatus*, K. (2½—4), L. T., Lil. 388; Umb. 177; Clem. 1; Thal. 2; Ran. 7; Papav. 20, 21; Cruc. 29; Bry. 171†; Rhus 88; Rut. 84; Geran. 79; Cary. 63; Ros. 150, 149, 134, 135;

<sup>1</sup> Dr. Kriechbaumer tells me that the species described by Kirby and later authors as *H. quadricinctus*, F., is not the true *H. quadricinctus* of Fabricius, but a distinct species, *H. tetrazonius*, Kl. But *H. quadristrigatus*, Latr. is identical with *H. quadricinctus*, F. and must receive that name, as the older one. (Gers-taecker, *Archiv für Naturgeschichte*, Jahrg. xxxiv. Bd. i.)

<sup>1</sup> According to F. Smith = *H. tumulorum*, L.

- 131; Papil. 126; Bor. 301, 300†, Scroph. 318, 322; Lab. 362†, Eric. 285; Caprif. 201, 202, 200; Scab. 211; Comp. 274, 262 (31 visits).
- Halictus sexsignatus*, Schenck, L., Ran. 7; Comp. 222, 274.
- *sexstrigatus*, Schenck, L., Papav. 21; Bry. 171†; Rhus 88; Ros. 149, 138, 139, 140, 141, 133; Scroph. 325; Lab. 346†; Eric. 285; Comp. 270 (13 visits).
- *Smeathmanellus*, K., L. T. Sld. Th., Umb. 185; Aq. 13; Res. 42; Geran. 78; Malv. 69; Scroph. 319, 321†; Camp. 277; Comp. 257, 246, 262, 271, 272, 273 (14 visits).
- *tarsatus*, Schenck, L., Pap. 98; Comp. 248 (2 visits).
- *villosulus*, K. = *punctulatus*, K., L. T. Th., Ran. 7; Cist. 45; Ros. 135, Convolv. 311; Jas. 283; Comp. 225, 229, 266, 267, 264, 265, 274, 271, 272, 273, 270 (16 visits).
- *zonulus*, Sm. (4), L. Tekl. Th., Sed. 164; Ran. 7; Resed. 42; Geran. 76; Malv. 69; Ros. 152, 149, 135, 142, 131; Papil. 101, 112; Bor. 301, 308; Scroph. 321†, 322; Lab. 366\*; Prim. 290\*; Comp. 257, 238, 274, 262 (22 visits).
- *spec.*, L., Cruc. 31; Geran. 80; Cary. 60, 53; Ros. 145; Ascl. 295†; Plant. 367, 368; Valer. 208 (10 visits).
- Heriades truncorum*, L. (4—4½), L. T. Th., Umb. 187; Papil. 96; Ol. 292; Scab. 211; Comp. 248, 246, 225, 228, 238, 223, 263, 264 (13 visits).
- Macropis labiata*, Pz. (2½—3), L., Umb. 187; Rhamn. 86; Ros. 135; Prim. 290.
- Megachile* (9 species, 77 visits).
- Megachile argentata*, F., (6) L., Jas. 283; Comp. 266.
- *centuncularis*, L. (6—7), L. Sld. Th., Lil. 388; Sed. 162; Umb. 194; Diel. 22†; Lythr. 165; Ros. 149; Papil. 108\*; Bor. 301; Scroph. 321†; Lab. 336; Caprif. 201, 203; Scab. 211; Comp. 257, 253, 246, 244, 224, 276 (20 visits).
- *circumcincta*, K. (8), L. Sld. Th., Sed. 162; Ros. 148, 149; Papil. 90, 100, 92, 108, 107, 117, 116; Ech. 310; Scroph. 335; Lab. 340; Plant. 368; Scab. 211; Comp. 242 (16 visits).
- *lagopoda*, L. (10), Th., Umb. 191; Comp. 242, 257, 255, 251, 246 (6 visits).
- *ligniseca*, K., L. Th., Malv. 69; Comp. 258.
- *maritima*, K., L. (8—9), Sed. 163; Papil. 101, 92, 120, 117; Scroph. 320; Scab. 211; Jas. 283; Comp. 259, 250 (9 visits).
- Megachile pyrina*, Lep. = *M. fasciata*, Sm.<sup>1</sup> (9), L. Sld. Th., Papil. 90, 93, 92\*, 124; Lab. 364, 346, 336 (7 visits).
- *versicolor*, Sm., L. Sld. Th., Pap. 92, 108, 120, 117; Comp. 246 (5 visits).
- *Willughbiella*, K. (6½—7), L. Sld. Th., Malv. 69; Papil. 90, 98, 108\*, 117; Ech. 310; Lab. 354, 336; Scab. 211; Comp. 266 (10 visits).
- Melecta armata*, Pz. = *punctata*, K. (11), L. T., Lab. 358, 361.
- *luctuosa*, Scop. (10), L. Th., Ech. 310.
- Nomada* (21 species, 85 visits).
- Nomada alternata*, K. = *N. Marshamella*, K., L., Comp. 274.
- *armata*, Schaeff. = *N. cineticornis*, Nyl., L., Scab. 211.
- *Fabriciana*, L., L., Coryd. 23†; Ros. 135; Scab. 211; Jas. 283; Comp. 267.
- *ferruginata*, K., L. Sld. Th., Sed. 162; Umb. 194; Papil. 94; Eric. 285; Comp. 238.
- *flavoguttata*, K., L., Cary. 65; Comp. 217, 274.
- *furva*, Pz. = *minuta*, F., L., Comp. 238.
- *germanica*, Pz., L. T., Lab. 340; Comp. 266.
- *Jacobaea*, Pz. (4), L., Onagr. 166; Lab. 358; Scab. 311; Jas. 283; Comp. 248.
- *lateralis*, Pz., L. Th., Umb. 195; Cruc. 30; Hyper. 68; Malv. 69; Ros. 135; Scroph. 330.
- *Lathburiana*, K. = *rufiventris*, K., L., Salix 378; Comp. 274.
- *lineola*, Pz. (6), L., Cruc. 30; Salix 378; Hyper. 68; Ros. 135; Scab. 317; Jas. 326; Comp. 248, 217, 274.
- *nigrita*, Schenck, L., Jas. 283; Comp. 248.
- *Roberjeotiana*, Pz., L. Th., Umb. 172; Onagr. 166; Jas. 283; Comp. 349.
- *ruficornis*, L. = *flava*, Pz. (3—4½), L. Sld., Salix 378; Cary. 65; Ros. 152, 161, 135, 138, 139; Pap. 90; Eric. 285; Jas. 283; Comp. 225, 274.
- *sexfasciata*, Pz. (7), L., Orch. 384; Ros. 138; Ech. 310.
- *solidaginis*, Pz., L. T., Papil. 94; Eric. 286\*; Comp. 248, 220.
- *signata*, Jur., L., Salix 378; Ros. 152, 153, 139; Comp. 274.
- *succincta*, Pz. (6½—7), L., Salix 378; Ros. 140, 127; Comp. 257, 274.

<sup>1</sup> According to Dr. Kriebhaumer identical with *M. pyrina*, Smith, but not with *M. pyrina*, Lep., identical, however, with *M. ericetorum*, Lep., which name is the oldest, and has priority over *M. fasciata*, Sm.

- Nomada varia*, Pz. = *fucata*, Pz. (5½—6),  
L. Th., Salix 378; Papil. 94; Lab. 349;  
Jas. 283; Comp. 238, 274, 276.  
— *xanthosticta*, K., L., Ros. 140.  
— *zonata*, Pz., L. T. Th., Comp. 225,  
276.

*Osmia* (13 species, 100 visits).

- Osmia adunca*, Latr. (10), L. T. Sld. Th.,  
Pap. 117; Ech. 310.  
— *ænea*, L. (9—10), L. Sld. Th.,  
Malv. 69; Papil. 90, 100, 92; Ech.  
310; Scroph. 320; Lab. 366, 364, 359,  
349, 336; Scab. 211; Comp. 258, 246.  
— *aurulenta*, Pz. (8—9), Sld. Th.,  
Pap. 90, 94, 91, 92, 116; Lab. 364;  
Comp. 246.  
— *cæmentaria*, Gerst. = *Spinolar*,  
Schenck, Th., Papil. 101; Ech. 310.  
— *cornuta*, Latr. (8—9), L., Ros. 129.  
— *fulviventris*, Pz., L. Th., Lab. 364;  
Scab. 211; Comp. 255, 245, 246.  
— *fusca*, Chr. = *bicolor*, Schr. (8),  
L. Sld. T. Th., Orch. 384; Ran. 4, 8;  
Viol. 49; Geran. 78; Ros. 135, 139;  
Papil. 112; Ech. 310; Pulm. 304;  
Lab. 366, 349; Comp. 274.  
— *interrupta*, Schenck, L. Th., Papil.  
90.  
— *leucomelæna*, K. (♂ 2½, ♀ 3¼—4),  
L., Ech. 310; Scroph. 320; Comp. 225.  
— *pilicornis*, Sm., L., Pulm. 304.  
— *rufa*, L. = *bicornis*, L. (7—9), L.  
T., Lil. 394, 388; Ir. 387†; Orch. 383;  
Clem. 1; Ran. 7, 11; Dicl. 22†; Cruc.  
30; Viol. 47, 49; Salix 378; Æsc.  
87; Geran. 77; Cary. 66, 57; Ros.  
150, 153, 133, 127, 129; Papil. 118†,  
119; Ech. 310; Bor. 304; Lab. 366,  
349, 346, 347, 336; Vinc. 291, 293;  
Prim. 288\*; Eric. 285; Comp. 217,  
274 (37 visits).  
— *spinulosa*, K. (5). Abundant in  
Thuringia, nesting in empty shells of  
*Helix ericetorum*. Papil. 116; Comp.  
257, 258, 255, 246, 225, 238, 263, 264,  
276, 262, 260 (12 visits).  
— *spec.*, L., Pap. 96.  
— *villosa*, Schenck (according to Dr.  
Kriechbaumer, identical with *O. platy-*  
*cera*, Gerst.), Sld., Papil. 108.

*Panurgus* (2 species, 16 visits).

- Panurgus Banksianus*, Latr. = *P. ater*,  
Latr. (3), L. T. Th., Comp. 263, 265,  
276, 270.  
— *calcaratus*, Scop. = *P. lobatus* F. (3),  
L. T. Th., Ran. 7; Onagr. 169; Comp.  
266, 267, 268, 263, 265, 276, 262, 271,  
273, 270 (12 visits).

*Prosopis* (15 species, 88 visits).

- Prosopis annularis*, Sm., Th., Lil. 388;  
Res. 42.  
— *armillata*, Nyl. (1½), L. T. Sld., Sed.  
162; Umb. 173, 192, 194, 186; Cruc.  
38; Res. 42, 43; Hyper. 68; Polygon.  
371; Ros. 140; Comp. 271 (13 visits).  
— *brevicornis*, Nyl., L., Sed. 162; Umb.  
177.  
— *clypearis*, Schenck., Th., Umb. 179.  
— *communis*, Nyl. (1—1½), L. T. Th.,  
Umb. 177, 179, 192, 186; Cruc. 38;  
Res. 42, 43; Rhus 89; Geran. 76, 77;  
Malv. 69; Cary. 63; Ros. 148, 149, 135,  
138, 130; Scroph. 317, 327; Lab. 346†;  
347†; Jas. 283; Comp. 248, 229 (24  
visits).  
— *dilatata*, K., L., Malv. 69; Jas.  
283.  
— *excisa*, Schenck., L., Ros. 135.  
— *hyalinata*, Sm. = *P. confusa*, Nyl.,  
L. Th., Ran. 7; Geran. 77; Malv. 69;  
Cary. 63; Ros. 140; Ech. 310; Camp.  
277, 278, 279, 282; Jas. 283; Comp.  
248.  
— *pictipes*, Nyl., L., Res. 42; Malv.  
69; Jas. 283; Comp. 225.  
— *propinqua*, Nyl., L., Ros. 149.  
— *punctulatissima*, Sm. = *P. obscurata*,  
Schenck, Th., Lil. 4; Comp. 246.  
— *signata*, Pz. (1½), L. Th., Umb. 173;  
Clem. 1; Thal. 22; Res. 42; Malv. 69;  
Ros. 343; Scroph. 317; Comp. 233 (8  
visits).  
— *sinuata*, Schenck, L. Th., Umb. 192,  
195; Rut. 84; Comp. 248.  
— *variegata*, F., L. Th., Sed. 162;  
Umb. 188, 191, 190, 195; Ros. 135;  
Jas. 283; Comp. 248, 225.  
— *spec.*, L., Umb. 187, 190; Til. 73.  
*Psithyrus*. The species of this genus  
are referred to *Bombus*.  
*Rhophitoides canus*, Eversm. (2½—3),  
Th., Papil. 90, 94.  
*Rhophites halictula*, Nyl., L., Jasione  
283.  
— *vulgaris* (Dufourea), Schenck (2),  
T. Th., Comp. 263, 264, 265, 262,  
273, 279, 270.  
*Saropoda himaculata*, Pz. = *S. rotundata*,  
Pz. (9), L. Th., Hyper. 68; Lythr.  
165; Ech. 310; Scroph. 365; Lab. 340;  
Eric. 287; Jas. 283; Comp. 257, 255  
(9 visits).  
*Sphcodes gibbus*, L. (including *rufescens*,  
*ephippia*, etc.) (1½), L. T. Sld. Th., Sed.  
162; Gross. 158; Umb. 176, 181, 188,  
192, 194, 195, 183; Coryd. 22; Cruc.  
33; Salix 378; Geran. 78; Fagopyr. 369;  
Onagr. 166; Ros. 140; Jas. 283; Comp.  
248, 225, 229, 233, 234, 222, 217.  
269, 270 (28 visits).  
*Stelis aterrima*, Pz. (5—5½), Th., (

- 131; Papil. 126; Bor. 301, 300†, Scroph. 318, 322; Lab. 362†, Eric. 285; Caprif. 201, 202, 200; Scab. 211; Comp. 274, 262 (31 visits).
- Halictus sexsignatus*, Schenck, L., Ran. 7; Comp. 222, 274.
- *sexstrigatus*, Schenck, L., Papav. 21; Bry. 171†; Rhus 88; Ros. 149, 138, 139, 140, 141, 133; Scroph. 325; Lab. 346†; Eric. 285; Comp. 270 (13 visits).
- *Smeathmanellus*, K., L. T. Sld. Th., Umb. 185; Aq. 13; Res. 42; Geran. 78; Malv. 69; Scroph. 319, 321†; Camp. 277; Comp. 257, 246, 262, 271, 272, 273 (14 visits).
- *tarsatus*, Schenck, L., Pap. 98; Comp. 248 (2 visits).
- *villosulus*, K. = *punctulatus*, K., L. T. Th., Ran. 7; Cist. 45; Ros. 135, 229, 266, 267, 264, 265, 274, 271, 272, 273, 270 (16 visits).
- *zonulus*, Sm. (4), L. Tekl. Th., Sed. 164; Ran. 7; Resed. 42; Geran. 76; Malv. 69; Ros. 152, 149, 135, 142, 131; Papil. 101, 112; Bor. 301, 308; Scroph. 321†, 322; Lab. 366\*; Prim. 290\*; Comp. 257, 238, 274, 262 (22 visits).
- *spec.*, L., Cruc. 31; Geran. 80; Cary. 60, 53; Ros. 145; Ascl. 295†; Plant. 367, 368; Valer. 208 (10 visits).
- Heriades truncorum*, L. (4—4½), L. T. Th., Umb. 187; Papil. 96; Ol. 292; Scab. 211; Comp. 248, 246, 225, 228, 238, 223, 263, 264 (13 visits).
- Macropis labiata*, Pz. (2½—3), L., Umb. 187; Rhamn. 86; Ros. 135; Prim. 290.
- Megachile* (9 species, 77 visits).
- Megachile argentata*, F., (6) L., Jas. 283; Comp. 266.
- *centuncularis*, L. (6—7), L. Sld. Th., Lil. 388; Sed. 162; Umb. 194; Diel. 22†; Lythr. 165; Ros. 149; Papil. 108\*; Bor. 301; Scroph. 321†; Lab. 336; Caprif. 201, 203; Scab. 211; Comp. 257, 253, 246, 244, 224, 276 (20 visits).
- *circumcincta*, K. (8), L. Sld. Th., Sed. 162; Ros. 148, 149; Papil. 90, 100, 92, 108, 107, 117, 116; Ech. 310; Scroph. 335; Lab. 340; Plant. 368; Scab. 211; Comp. 242 (16 visits).
- *lagopoda*, L. (10), Th., Umb. 191; Comp. 242, 257, 255, 251, 246 (6 visits).
- *ligniseca*, K., L. Th., Malv. 69; Comp. 258.
- *maritima*, K., L. (8—9), Sed. 163; Papil. 101, 92, 120, 117; Scroph. 320; Scab. 211; Jas. 283; Comp. 259, 250 (9 visits).
- Megachile pyrina*, Lep. = *M. fasciata* (9), L. Sld. Th., Papil. 90, 124; Lab. 364, 346, 336 (7 visits).
- *versicolor*, Sm., L. Sld. Th., 92, 108, 120, 117; Comp. 248 (10 visits).
- *Willughbiella*, K. (6½—7), L. Th., Malv. 69; Papil. 90, 92, 117; Ech. 310; Lab. 354, 336; Comp. 211; Comp. 266 (10 visits).
- Melecta armata*, Pz. = *punctata*, K., L. T., Lab. 358, 361.
- *luctuosa*, Scop. (10), L. Th., 310.
- Nomada* (21 species, 85 visits).
- Nomada alternata*, K. = *N. Marshamensis*, K., L., Comp. 274.
- *armata*, Schaeff. = *N. cincticornis*, Nyl., L., Scab. 211.
- *Fabriciana*, L., L., Coryd. 23†; Ech. 135; Scab. 211; Jas. 283; Comp. 266.
- *ferruginata*, K., L. Sld. Th., Sed. 162; Umb. 194; Papil. 94; Eric. 285; Comp. 238.
- *flavoguttata*, K., L., Cary. 65; Comp. 217, 274.
- *furva*, Pz. = *minuta*, F., L., Comp. 238.
- *germanica*, Pz., L. T., Lab. 349; Comp. 266.
- *Jacobaeae*, Pz. (4), L., Onagr. 166; Lab. 358; Scab. 311; Jas. 283; Comp. 248.
- *lateralis*, Pz., L., Th., Umb. 195; Cruc. 30; Hyper. 68; Malv. 69; Ros. 135; Scroph. 330.
- *Lathburiana*, K. = *rufiventris*, L., L., Salix 378; Comp. 274.
- *lineola*, Pz. (6), L., Cruc. 30; Salix 378; Hyper. 68; Ros. 135; Scab. 311; Jas. 326; Comp. 248, 217, 274.
- *nigrita*, Schenck, L., Jas. 283; Comp. 248.
- *Roberjeotiana*, Pz., L. Th., Umb. 172; Onagr. 166; Jas. 283; Comp. 349.
- *ruficornis*, L. = *flava*, Pz. (3—4½), L. Sld., Salix 378; Cary. 65; Ros. 152, 161, 135, 138, 139; Pap. 90; Eric. 285; Jas. 283; Comp. 225, 274.
- *sexfasciata*, Pz. (7), L., Orch. 334; Ros. 138; Ech. 310.
- *solidaginis*, Pz., L. T., Papil. 94; Eric. 286\*; Comp. 248, 220.
- *signata*, Jur., L., Salix 378; Ros. 152, 153, 139; Comp. 274.
- *succincta*, Pz. (6½—7), L., Salix 378; Ros. 140, 127; Comp. 257, 274.

<sup>1</sup> According to Dr. Kriechbaumer identical with *M. pyrina*, Smith. but not with *M. pyrina* Lep., identical, however, with *M. erichsonii* Lep., which name is the oldest, and has priority over *M. fasciata*, Sm.

- Gorytes campestris*, L.<sup>1</sup> (1), L. Sld., Umb. 179, 177, 194; Parn. 157; Rhys. 88.  
 — *mystaceus*, L. (1), L. T., Clem. 1; Bry. 171; Ros. 134.  
*Hoplisus laticinctus*, Lep.<sup>1</sup> (1), Th., Umb. 179, 185.  
*Lindenius albilabris*, F., L., Lab. 340; Jas. 283; Comp. 248, 253, 225.  
*Mellinus arvensis*, L., L., Comp. 234.  
 — *sabulosus*, Dlb., L., Jas. 233.  
*Mimesa bicolor*, Shuck, Th., Umb. 194.  
 — *unicolor*, v. d. L., L. Th., Umb. 194.  
*Miscus campestris*, Latr. (4), L. Th., All. 393; Ros. 135; Jas. 283.  
*Mutilla europæa*, L. (1½), Th., Umb. 193, 195.  
*Myrmosa melanocephala*, F., L. Th., Umb. 179, 192, 183.  
*Nysson maculatus*, v. d. L., Th., Umb. 191.  
*Oxybelus bellicosus*, Ol., L., Umb. 179, 196; Jas. 283.  
 — *bellus*, Dlb. (14 *guttatus*, Sh.), L., Sed. 162; Umb. 179; Cruc. 38; Rut. 84; Ros. 141, 142; Comp. 225.  
 — *bipunctatus*, Ol., L., Umb. 179, 188, 195.  
 — *mandibularis*, Dlb., L., Jas. 283.  
 — *trispinosus*, F., L., Comp. 248, 225, 229.  
 — *uniglumis*, L. (1½), L. T., Sed. 162; Umb. 179, 192, 194, 196, 195, 186; Clem. 1, 7; Cruc. 38; Rhys. 88; Til. 73; Cary. 55; Ros. 135, 138, 140, 141, 142, 133; Jas. 283; Comp. 248, 225, 229, 233 (23 visits.)  
 — spec., L., Geran. 79.  
*Passalæcus monilicornis*, Dlb., L., Ros. 133.  
*Philanthus triangulum*, F. (2—2½), L. Th., Umb. 172, 179, 190, 194; Jas. 283; Comp. 248, 225.  
*Pompilus chalybeatus*, Schi., L., Comp. 225.  
 — *cinctellus*, v. d. L., Th., Umb. 192.  
 — *intermedius*, Schenck, L. Th., Umb. 195, 184.  
 — *neglectus*, Wesm., L. Th., Umb. 179, 192, 195, 185; Ros. 133.  
 — *niger*, F., L. T., Umb. 179, 195.  
 — *pectinipes*, v. d. L., L. T. Th., Umb. 194, 186, 183.  
 — *plumbeus*, Dlb., L., Comp. 225.  
 — *rufipes*, F., L., Jas. 283; Comp. 225.  
 — *spissus*, Schi., L., Umb. 179, 186.  
*Pompilus trivialis*, Kl., L., Umb. 188, 174; Fagop. 369; Comp. 225.  
 — *viaticus*, Scop.<sup>1</sup> (F., not L.!) (1—1½), L. Sld. Th., Umb. 188, 189, 191, 194, 195, 185; Parn. 157; Hott. 289; Jas. 283; Comp. 225, 222, 264, 271.  
 — spec., L., Corn. 197.  
*Priocnemis bipunctatus*, F.,<sup>2</sup> Th., Umb. 172, 191.  
 — *exaltatus*, F., Th., Umb. 194.  
 — *obtusiventris*, Schi., Th., Umb. 191, 195.  
*Psammophila affinis*, K.<sup>3</sup> L. Th., Pap. 101; Ech. 310; Lab. 348; Ascl. 295; Scab. 211; Jas. 283; Comp. 259, 255.  
 — *viatica*, L., L. Th., Umb. 191; Veron. 327; Scab. 211.  
*Psen atratus*, Pz. (½—¾), L. Th., Umb. 192; Ros. 133.  
*Rhopalum clavipes*, L., L., Rut. 84.  
*Salius sanguinolentus*, F., L., Comp. 248.  
*Scolia bicincta*, hortorum, 4 *punctata* (¾), Ascl. 295.  
*Tachytes pectinipes*, v. d. L.,<sup>4</sup> L. Th., Umb. 191, 192; Jas. 283.  
 — *unicolor*, Pz., Th., Umb. 192.  
*Tiphia femorata*, F., L. Th., Umb. 172, 191, 192, 193, 194, 195.  
 — *minuta*, v. d. L., L., Cruc. 27; Rut. 84.  
 — *ruficornis*, Kl. (1), L., Umb. 188.  
*Trypoxylon clavicerum*, Latr. (½), Th., Umb. 192.  
 — *figulus*, L. (½), L., Rut. 84.  
*G. Tenthredinidæ* (38 species, 125 visits).  
*Athalia roseæ*, L., L. Th., Umb. 178, 188, 190, 194, 195, 185, 183.  
 — *spinarum*, F., L., Umb. 177; Fagop. 369.  
*Cephus pallipes*, Kl., L., Ran. 8; Cary. 65.  
 — *spinipes*, Pz., L., Ran. 7; Cruc. 40.  
 — *troglydites*, L., L., Umb. 177.  
 — spec., L., Ran. 7, 8; Cruc. 40; Comp. 267, 274.  
*Cimbex sericea*, L., L. Sld., Umb. 179, 177, 181, 194; Comp. 229.  
*Dolerus cenchris*, Htg., T., Umb. 183.  
 — *eglanteriæ*, F. (¾—1), L., Umb. 177; Salix 378, 379.

<sup>1</sup> According to Frederick Smith the original specimens of *Gorytes campestris*, L., in Linnaeus' collection are only males of *G. mystaceus*, L.; and the insect called *G. campestris*, L., in this book must be called *G. Fargei*, Shuck.

<sup>2</sup> According to Frederick Smith the specimens of this species in Linnaeus' collection are identical with *Spheg fusca*, L., and the species must therefore be called *P. fusca*, L.

<sup>3</sup> According to F. Smith = *P. variabilis*, Rossi.

<sup>4</sup> According to F. Smith this species, from the original type-specimens in Fabricius' collection in Kiel, is identical with *P. lataria*, F., which name has priority.

<sup>5</sup> According to F. Smith the Linnæan type-specimens of *Spheg pectinipes*, F., show it to be a *Pompilus*, and what is called *Tachytes pectinipes*, L., in this book, must be called *T. pompiliformis*, Pz.

— <i>ustulata</i> , L., L. Sld., Umb. 179, 194, 14.	Sld.
— <i>vulgaris</i> , Kl., L. Th., Umb. 179, 194.	Polist Th.
<i>Macrophya neglecta</i> , Kl., T., Umb. 185.	Scro
<i>Nematus caprae</i> , L., L., Ros. 151.	Syn
— <i>hortensis</i> , Htg., L., Umb. 185.	Pteroc
— <i>myosotidis</i> , F., T., Umb. 185.	225.
— <i>rufescens</i> , H., L., Salix 378.	Vespa
— <i>vittatus</i> , Lep., L., Umb. 185, 174.	Scro
<i>Selandria serva</i> , F. (j-1), L., Umb. 179, 177, 181, 194, 195, 185.	— h 194
<i>Tarpa cephalotes</i> , F., Th., Comp. 238.	287
<i>Tenthredo annulata</i> , F., L., Umb. 194, 185.	— n Sym
— <i>atra</i> , L., L., Umb. 179.	— r
— <i>bicincta</i> , L., L. Sld., Umb. 181; Ros. 133.	18; 201.
— <i>bifasciata</i> , L., L. Th., Umb. 179, 177, 181, 194, 183.	— s
— <i>flavicornis</i> , L., T., Umb. 179, 184, 182.	— v Scro
— <i>marginella</i> , Kl., L., Rhus 88.	V. L
— <i>notha</i> , Kl. (1½), L. T. Th., Sed. 164; Umb. 179, 177, 181, 178, 189, 194, 196, 195, 185, 184, 183; Comp. 238, 225, 229, 227.	A.
— <i>rapae</i> , Kl., L., Umb. 185; Rubiac. 206.	Dasych 202*
— <i>rustica</i> , L., L. T., Umb. 185, 184; Ros. 134.	Eucheli Forthes
— <i>scrophulariae</i> , L., L. T., Onagr. 166; Comp. 225, 229.	B. Micr
— <i>tricincta</i> , F., L. T., Umb. 177, 194.	Adela s
— <i>spec.</i> , L. Th., Umb. 179, 177, 181, 192, 193, 194, 185, 184, 183, 174; Hyper. 68*; Ros. 134; Papil. 96*; Comp. 248, 225, 229, 272.	— sp Lab. Ephesti 317.
	Botys f
	Jas. f
	— ne Tortrix
H. <i>Vespidæ</i> (18 species, 74 visits).	C. J
<i>Eumenes pomiformis</i> , Rossi (2), L., Umb. 192; Bry. 171; Rhamn. 86; Rhus 88.	

- Euclidia glyphica*, L. (7), L., Ran. 7 ;  
Cruc. 40 ; Cary. 57 ; Papil. 90†, 94†,  
116† ; Scroph. 334 ; Lab. 366 ; Scab.  
211 ; Comp. 249.  
— *Mi*, L., L., Comp. 267.  
*Hadena didyma*, Esp., L., Comp. 234.  
*Mamestra serena*, S. V., Th., Scab. 211.  
*Plusia gamma*, L. (15), L. Th., Lin. 75 ;  
Dianth. 53, 54 ; Papil. 100, 94, 111†,  
122†, 116† ; Ech. 310 ; Bor. 302 ; Lab.  
353, 346† ; Eryth. 298 ; Caprif. 202 ;  
Scab. 212 ; Comp. 257, 259, 253, 246,  
244, 221, 271, 273 (23 visits).  
*D. Rhopalocera* (46 species, 259 visits).  
*Argynnis Aglaia*, L., Sld. Th., Lab. 340 ;  
Comp. 248, 237.  
— *Paphia*, L., Th. Westf., Umb. 190 ;  
Ros. 135 ; Lab. 371 ; Comp. 214.  
*Colias Hyale*, L., L. Th., Dianth. 53 ;  
Papil. 94 ; Ech. 310 ; Lab. 364 ; Scab.  
211 ; Comp. 257, 256, 271, 260.  
— (*Rhodocera*) *rhamni*, L., L. Sld.  
Th., Cruc. 30 ; Viol. 47, 48, 49 ;  
Dianth. 53 ; Lythr. 165 ; Papil. 122 ;  
Bor. 304 ; Lab. 366, 350 ; Comp. 249,  
274.  
*Hesperia (Syrichthus) alveolus*, Hb., L.  
Sld., Viol. 49 ; Papil. 90† ; Lab. 366 ;  
Comp. 229, 274.  
— *lineola*, O., L., Umb. 195 ; Scab.  
211 ; Comp. 214.  
— (*Carterocephalus*) *Paniscus*, Esp.,  
L., Ros. 135.  
— *silvanus*, Esp., L. Sld., Hyper. 68\* ;  
Malv. 72 ; Cary. 59 ; Papil. 100, 122 ;  
Ech. 310 ; Lab. 355 ; Comp. 248, 253,  
225, 272.  
— (*Erynnis*) *Tages*, L., L., Papil. 90†.  
— *thaumas*, Hfn. (linea, S. V.), L.,  
Papil. 100, 101, 94† ; Bor. 303 ; Jas.  
283 ; Comp. 257, 223.  
— spec., L. Th., Delph. 15† ; Viol.  
49 ; Papil. 98†, 94† ; Lab. 366 ; Comp.  
229, 274.  
*Lycæna Ægon*, S. V., L., Jas. 283 ;  
Comp. 225.  
— *Alsus*, S. V., Th., Papil. 91\* ; Comp.  
221.  
— *Argiolus*, L., L., Salix 378 ; Papil.  
94 ; Lab. 355 ; Eric. 285 ; Comp. 267.  
— *Icarus*, Rott. (Alexia, S. V.), L., Ran.  
7 ; Cary. 57 ; Papil. 90† ; Bor. 307 ;  
Lab. 340 ; Comp. 268.  
— spec., L. Th., Papil. 94†, 116† ;  
Ech. 310 ; Comp. 257, 223, 214.  
*Melitæa Athalia*, Esp., Sld. Th., Lil.  
391 ; Papil. 355 ; Comp. 258, 230.  
— *Cinxia*, L. (10), L., Ech. 310.  
*Papilio Machaon*, L. (18), L. Th., Lil.  
391 ; Ol. 291 ; Scab. 210.  
— *Podalirius*, L., L., Lab. 366 ; Ol.  
291.  
*Pieris brassicæ*, L. (15), L. Th., Cruc.  
30, 34 ; Viol. 48 ; Fagop. 369 ; Cary.  
57, 59 ; Ros. 129 ; Papil. 98†, 100, 94 ;  
Ech. 310 ; Bor. 309 ; Lab. 366, 364,  
353, 349, 348 ; Ol. 291 ; Comp. 257,  
248, 250, 253, 246, 267, 264, 275, 262  
(27 visits).  
— (*Anthocharia*) *cardamines*, L. (11—  
12), L., Cruc. 30 ; Viol. 48 ; Ol. 291.  
— *cratægi*, L. (17), L., Ros. 135.  
— *napi*, L. (11), L., Cruc. 30, 34, 36 ;  
Viol. 48, 49 ; Bry. 171 ; Geran. 82 ;  
Fagop. 369 ; Cary. 65 ; Ros. 135 ;  
Papil. 115† ; Bor. 309 ; Lab. 366 ;  
Ol. 291 ; Comp. 257, 253, 245, 225,  
266, 274 ; Valer. 209 (23 visits).  
— *rapæ*, L. (12), L., Umb. 196 ; Cruc.  
34, 36 ; Viol. 48, 49 ; Geran. 76 ;  
Malv. 69 ; Polygon. 371 ; Dianth. 52 ;  
Cary. 57 ; Lythr. 165 ; Ros. 129 ; Pa-  
pil. 100, 94, 121, 122, 117 ; Lab. 366,  
353 ; Ol. 291 ; Scab. 212 ; Comp. 253,  
245, 214, 262 (25 visits).  
*Polyommatus dorilis*, Hfn. (Circe, S. V.),  
L., Jas. 283 ; Comp. 234, 223, 221,  
217.  
— *Eurydice*, Rott., L., Polygal. 51.  
— *phleas*, L., L. Th., Ran. 7 ; Fagop.  
369 ; Cary. 60, 53 ; Scab. 212 ; Jas.  
283 ; Comp. 330, 346, 234, 238 (10  
visits).  
*Satyrus (Pararga) Egeria*, L., Westf.,  
Comp. 214.  
— (*Epinephele*) *Galatea*, L., Westf.,  
Comp. 257, 255, 214.  
— (*Epinephele*) *Hyperanthus*, L., L.  
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— (*Epinephele*) *Janira*, L. (10), L.,  
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— (*Erebia*) *Medea*, S. V., Sld., Scab.  
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— (*Erebia*) *Medusa*, S. V., Westf.,  
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— (*Pararga*) *Megara*, L., L., Papil.  
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— (*Cœnonympha*) *Pamphilus*, L., L.  
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— *C-album*, L. (11), L., Umb. 18.  
— *cardui*, L., L. Th., Lab. 34.  
— *lo*, L. (15—16), L. Sld.  
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— *urticæ*, L. f.  
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122; Lab. 364; Ol. 291; Scab. 211; Comp. 255, 248, 237, 218, 266, 275 (15 visits).

*E. Sphingæ* (14 species, 48 visits).

*Ino Statice*, L., L. T. Sld., Cary. 57; Onagr. 166; Scab. 211; Camp. 277; Jas. 283; Comp. 229.

*Macroglossa fuciformis*, L., L., Cary. 57; Lab. 366, 349; Ol. 291.

— *stellatarum*, L., L. Sld. Th., Dianth. 53; Onagr. 169; Ech. 310; Lab. 364, 349; Eryth. 298; Ol. 291; Comp. 255.

*Sesia asiliformis*, Rott. (*S. cynipiformis*, Esp.), Th., Papil. 94†; Comp. 238.

— *empiformis*, Esp., Sld. Th., Papil. 90†; Lab. 340.

— *tipuliformis*, L., L. T., Cruc. 38; Lab. 340; Comp. 232.

*Sphinx convolvuli*, L. (65—80), L., Convolv. 311\*; Caprif. 202.

— (*Deilephila*) *Elpenor*, L. (20—24), L., Caprif. 202.

— *ligustri*, L. (37—42, L.), Sapon. 56; Caprif. 202.

— *pinastri*, L. (28—33), L., Caprif. 202.

— (*Deilephila*) *Porcellus*, L. (20), L., Cary. 58; Caprif. 202.

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*Zygæna carniolica*, Scop. (*Zonobrychis* S. V.), Th., Dianth. 53; Pap. 94†, 119†; Comp. 257, 258, 248, 249.

— *Ioniceræ*, Esp., L. Th., Papil. 90†; Ech. 310; Scab. 211; Comp. 247, 257.

#### VI. NEUROPTERA (4 species, 13 visits).

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*Hemerobius* spec., L., Umb. 195, 185.

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*Sialis lutaria*, L., L., Umb. 177, 185.

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*Forficula auricularia*, L., L., Papav. 20; Camp. 282.

*Podura* spec., L., Convolv. 311\*.

#### VIII. THYSANOPTERA (18 visits).

*Thrips* spec., L., Ran. 9, 10; Cruc. 30, 39; Res. 42; Cary. 65, 66, 60, 63; Lythr. 165; Ros. 151, 138; Convolv. 311\*; Scroph. 317; Lab. 339; Vinc. 293; Eric. 287.

#### SUMMARY OF INSECT-VISITS NOTED IN THIS BOOK.

Coleoptera .....	129	species with	469	visits.
Diptera .....	253	"	1598	"
Hemiptera .....	6	"	15	"
Hymenoptera ...	368	"	2750	"
Lepidoptera ....	79	"	365	"
Neuroptera .....	4	"	13	"
Orthoptera.....	3	"	3	"
Thysanoptera ...	1	"	18	"

Altogether... 843 species, with 5231 different visits.

## INDEX OF PLANTS,

### WITH THE NUMBER OF THEIR INSECT-VISITORS.

ABBREVIATIONS.—*Coleopt.* = Coleoptera; *Dipt.* = Diptera in general; *Musc.* = Muscidae; *Syrph.* = Syrphidae; *Rhing.* = Rhingia; *Hemipt.* = Hemiptera; *Hymen.* = Hymenoptera, not including the bees; *Apid.* = Apidae in general; *A\**. = *Apis mellifica*; *B.* = *Bombus* and *Anthophora* (the longest-tongued of our bees); *Lepid.* = Lepidoptera in general; *Lepid. d.* = diurnal Lepidoptera; *Lepid. n.* = nocturnal Lepidoptera; *Neuropt.* = Neuroptera; *Orthopt.* = Orthoptera; *Th.* = Thrips.

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